THE ONTOGENY OF PREDATORY BEHAVIOUR

IN THE GOLDEN HAMSTER (M.a.auratus)

A Thesis submitted by

Richard Henry Polsky

A Candidate for the Degree of Doctor of Philosophy

––––––––––––––––––––

UMI Number: U418013

UMI

Dissertation Publishing

ProQuest

ACKNOWLEDGEMENTS

I am indebted to the following for their assistance during the course of my studies at Leicester:

First, I extend thanks to the late Professor S. G. M. Lee for taking me on as a post-graduate. The project supervisor, Professor W. Sluckin, I thank for his sincere interest and throughout he remained very encouraging and thoughtful. Dr. U. Weidmann also provided encouragement and criticism and was always willing to help in an advisory capacity. Dr. R. H. Porter, an American post-doctoral fellow, Dr. J. C. Berryman and C. Fullerton, research personnel, and several post-graduates provided, in part, an enjoyable atmosphere in which to work.

Second, I am grateful to G. Evans and the entire technical staff for helping in innumerable ways with the practical aspects of the project. D. McArthur and J. Ashworth were always at hand with intelligent suggestions when they were needed most. D. Mann, the animal technician, looked after the hamsters and locusts at crucial times and P. Kirkbride and B. Williamson helped chiefly with electrical matters.

Finally, I thank K. Garfield for the excellent photographs contained herein, M. Frape for coping with my importunate requests

Without the help of all the above, and others not mentioned,

it is unlikely that the project would have progressed as far as it

did.

CONTENTS

ILLUSTRATIONS

SYNOPSIS

The treatise opens with a literature review on predatory behaviour in mammals. Areas discussed included species of investigation, methods of investigation, behavioural patterns, developmental and motivational aspects, the effect of hormones and the stimuli involved in the control of the response. A conclusion which emerged was that more research was needed with species other than the albino rat.

This conclusion served as the impetus for experimentation on the ontogeny of predation in the golden hamster (M.a.auratus). In total, a pilot study, which focused on the qualitative aspects of the response, and 12 experiments were reported. The prey used throughout were nymphs of the species Locusta migratoria. The basic methodology consisted of introducing prey into a naive subject's own home cage and manually recording the following behaviours: latency to capture, and the frequency of prey exploration, withdrawal from the prey, nip at the prey and unsuccessful capture.

The principal findings showed that: 1) older hamsters were more likely to capture; 2) with the experience of several successful captures hamsters became more efficient captors; 3) hamsters as young as 20 days would capture in the normal adult manner; 4) the interval between successive prey presentations had a small but significant effect on the likelihood of capture; 5) prey removal after capture decreased the chance of subsequent capture in hamsters with weak dispositions to capture; 6) prey removal after capture had no effect on hamsters with strong dispositions; 7) the response of

capture could be 'primed' through prior sensory exposure to the prey;

8) prey-capture was susceptible to the effects of selective breeding.

The theory ascribed to these results was that prey-capture in the hamster was a species-typical behaviour founded upon certain pre-dispositions but nevertheless liable to the effects of experience. Therefore it was concluded: 1) for hamsters with weak dispositions to capture the pre-capture and post-capture experiences were both needed for the development of the response. The pre-capture phase (sensory exposure to prey and the performance of the behaviours involved in capture per se) served primarily to reduce fear and increase capture efficiency and the post-capture phase (prey consumption) served primarily to increase capture tendency; 2) for hamsters with strong dispositions to capture the development of predation was not dependent on eat after capture (the post-capture experience). This suggested that the pre-capture experience had self-reinforcing properties of its own.

Hamster predation was then discussed from a comparative viewpoint and mention was made of areas in need of investigation.

Der Abhandlung geht ein Literaturverzeichnis uber das Raubverhalten bei Saugetieren voran. Folgende Diskussionspunkte wurden hierbei berucksichtigt: die Tierarten, Untersuchungsmethoden, Verhaltensmuster, Entwicklungs- und Motivationsaspekte, Hormonwirkungen und die Gesichtspunkte, die bei der Reaktionskontrolle eine Rolle spielten. Es ergab sich die Schlu folgerung, da Untersuchungen an anderen Tierarten als der wei en Ratte vonnoten seien.

Diese Notwendigkeit fuhrte zu einer Untersuchungsreihe, die das Wesen des Raubverhaltens beim Goldhamster (M.a.auratus) zum Gegenstand hat. Im Ganzen gesehen, eine Pionierarbeit, die sich auf die qualitativen Aspekte der Reaktionen konzentrierte. Der Untersuchung liegen 12 Experimente zugrunde. Als Beute wurden Larven der Locusta migratoria verwandt. Das eigentliche Verfahren bestand in der Einfuhrung der Beute in den sonst unberuhrten Heimat-kafig des Untersuchungsobjekts und in den durch die Hand vorgenommenen Aufzeichnungen folgender Verhaltensaspekte: latente Fangneigung, Haufigkeit der Beuteuntersuchung, Ruckzug von der Beute, Nagen an der Beute und erfolgloser Fang.

Die Hauptergebnisse waren:

1. altere Hamster hatten bessere Fangaussichten,

2. die Erfahrung von verschiedenen erfolgreichen Fangen machte die Hamster zu tuchtigeren Jagern,

3. junge Hamster von 20 Tagen fangen in der gleichen Weise wie normale Erwachsene,

4. der Zwischenraum zwischen den aufeinanderfolgenden Darbietungen

der Beute hatte eine kleine aber bedeutende Wirkung auf die

Reaktionsentwicklung,

5. Beuteentzug nach dem Fang verminderte die Chancen nachfolgender

Fange bei Hamstern mit schwacher Fangdisposition,

6. Beuteentzug nach dem Fang hatte keine Wirkung auf Hamster mit

starker Fangdisposition,

7. Verbesserung des Fangverhaltens durch vorherige Fuhlungnahme

mit der Beute,

8. Der Beutefang stand in Verbindung mit den Merkmalen der

selektiven Aufzucht.

Die Theorie, die sich an diese Resultate knupfte, war, da

der Beutefang beim Hamster ein artenspezifisches Verhalten ist, das

auf einer bestimmten Veranlagung beruht, jedoch durch Erfahrung

beeinflu t wird. Deshalb kam man zu der Folgerung, da :

1. Erfahrungen, die vor und nach dem Fang gemacht werden, beide

fur die Hamster mit schwacher Fangdisposition notig sind fur die

weitere Verhaltensentwicklung. Die Phase vor dem Fang (erste

Fuhlungnahme mit der Beute und der Verhaltensvollzug, der sich

auf den eigentlichen Fang bezieht) dient in erster Linie dazu,

die Furcht zu vermindern und das Fanggeschick zu erhohen, wahrend

die Phase nach dem Fang (Beuteverzehr) vor allem dazu dient, die

Fangneigung zu erhohen,

2. fur Hamster mit starker Fangdisposition die Entwicklung des

Beutemachens nicht von dem Verzehr der Beute nach dem Fang

abhangig ist (die Erfahrung nach dem Beutefang). Dies la t

annehmen, da die Erfahrung vor dem Fang bereits ein Vermogen

zur Selbstbestatigung beinhaltet.

Das Beuteverhalten des Hamsters wurde dann von einem
vergleichenden Standpunkt aus gesehen. Dabei wurden Bereiche
erwahnt, die noch der Erforschung bedurfen.

SECTION I

BACKGROUND TO THE EXPERIMENTS

1

INTRODUCTION

Nearly five years ago when this author first started searching

for a research topic within the field of comparative psychology he

concerned himself initially with the vast subject matter of animal

aggression. A careful review of the literature on some of the more

commonly studied laboratory mammalian species, such as rats, mice

and cats, revealed that many new and interesting findings had come

about during the decade of the sixties; further, publications in

some of the recently dated journals and texts indicated that the

topic of aggression in mammals continued to be one of the most inten-

sively investigated areas amongst animal behaviourists.

Assimilation of a large number of studies further disclosed

that the bulk of the research concerned itself mainly with aggression

within species or what is more technically known as intra-specific

aggression. It appeared to this author that relatively little behavioural

work had been carried out on inter-specific aggression (e.g. between

species) in the form of the predator - prey interaction. Most of the

studies that existed concerned themselves with cats killing rats or

rats killing mice. The cat - rat interaction was first studied in

detail in the thirties by the late Zing-Yang Kuo and later by the

German ethologist Paul Leyhausen. Investigations into the rat - mouse

interaction were initiated by P. Karli in 1956 and subsequently

studied most thoroughly by James Myer in America at the Johns Hopkins

University. In general it seemed that nearly all of the research

concerned with the inter-specific predatory aggression of a labora-

tory mammal had been carried out with either rats or cats and in most

cases it was always a small rodent they encountered. With the excep-

tion of a small-scaled observational study reported on in 1969,

concerned with cricket killing by domestic mice, this author could

find no controlled investigation which examined a laboratory mammalian

species taking an insect.

Thus it appeared that there was much scope for research on the

topic of insect feeding, particularly by rodents. In a way this

author found it surprising for he knew that many rodents took insects

for food in the natural habitats and he further knew that rodents in

different parts of the world occasionally helped in the control of

harmful insects pests. However, it appeared that there was a paucity

of information on the actual behaviour involved in insect capture and

feeding.

For this reason the author became interested in the problem;

consequently he set out to investigate it experimentally and the

results of his findings form the subject matter of this treatise.

The rationale for selecting golden hamsters as the subjects of

study rests on the fact that as a species they are economically

feasible to maintain, they are available in large numbers for experi-

mental purposes, but of greater importance it was apparent that nothing was known about their predatory habits. The choice of hamsters also seemed sensible because it was further known that insects were indigenous to their natural habitat. Further discussion about this matter will be presented at a later point in Section I.

Mainly for practical reasons (availability, economics, care and breeding) the insects which served as prey in all of the experiments were of the species Locusta migratoria, more commonly known as the African migratory locust. However, as it will be mentioned, locusts are found in northern Syria, the home-grounds of the hamster; hence it is probable that the match-up of hamster versus locust was not a contrived biological situation but rather one which might well occur in the wild.

The treatise has been broken down into three sections. The first, a literature review, should provide the reader with the necessary background with which to approach the experiments. Section I, Chapter 2, initially focuses on the predator - prey interaction from a very general point of view and then subsequently focuses specifically on the behaviour of the predator. In this chapter both ethological and psychological literature is covered. Chapter 3 introduces the hamster as the subject of study. Literature pertaining to its feeding habits will be reviewed and, in addition, a description of the initial pilot study this author undertook will be presented. Section II deals with the experiments themselves. In total 12 experiments are reported and as one reads through them it should

become obvious that all are concerned with the developmental aspects

of the predatory response. The experiments attempted to answer

fundamental questions about ontogeny such as the influence of age

and experience, the reinforcing effects of feeding on captured and

dead prey and the underlying genetic basis. Finally, in Section III

a general discussion will be presented with special attention being

paid to the comparative aspects of hamster predatory behaviour.

2

THE INTERACTION BETWEEN PREDATOR AND PREY

2.1. SOCIAL ASPECTS OF THE INTERACTION

Let us begin by considering the interaction between two
rodents who happen to meet in a small enclosed neutral area like
the open field. How, one may ask, might they behave? If, for
example, they are laboratory rats then there is a good chance
that they would be strongly attracted to each other. For instance,
it is quite possible that each would respond with much amicable and
investigative behaviour. Sniffing each other's genitals, grooming,
'climbing over and under' are all likely occurrences. If the rats
were the opposite sex and if the female was receptive then possibly
copulation would occur. Regardless of how the behaviour of each of
these rats be classified, i.e. whether it be regarded as investiga-
tive, friendly or sexual, it is important to realize that, very
generally, each animal in this interaction mutually and reciprocally
influences the other's behaviour, hence the behaviour of each must
be regarded as something which is social. Further, since this
interaction involves two animals then we may regard it very broadly
as a relationship and a social one at that.

If this be the case, how then might this social relationship be defined? Let us turn to the well-known J.P.Scott for a definition. Very simply he defines a social relationship as the "regular and predictable behaviours exhibited by two individuals, usually of the same species" (1964, p-233). If one scrutinizes this definition it becomes apparent that much of the value and usefulness of it rests on the words regular and predictable. Scott identifies nine such regular and predictable behaviours and he presents definitions for each. For instance, there is the investigative type of behaviour which is regarded as the investigation of the social, biological and physical environments. Agonistic behaviour is another type and it is regarded as any behaviour associated with conflict which includes fighting, escape and freezing. Eating and drinking are categorized as ingestive types of behaviour and additional types include allelomimetic (e.g. contagious behaviour), et-epimeletic (care soliciting behaviour), epimeletic (care giving behaviour), sexual, eliminative and shelter seeking. Very generally, Scott views each of these regular and predictable behaviours as gross behavioural adaptations for each allows the individual to adjust to fluctuations in its social and non-social environments.

Returning to the definition of a social relationship presented above it becomes evident that the various types of regular and predictable behaviours comprise or combine to form a social relationship. Fundamentally then, in Scott's own words, "social behaviour determines social relationships" (1958, p-162). So, for example, when two animals fight or engage themselves in behaviour associated with fighting

(e.g. the agonistic type of social behaviour) then they may be

regarded to be involved in what Scott calls the social relationship

of dominance-subordination. Often, however, social relationships

are more complex than the relatively simple dominance-subordination

relationship for most involve not just a single type of social

behaviour but, instead, the amalgamation of several types. For

instance, the social relationship of care dependency, such as

parental care in birds and mammals, involves epimeletic, ingestive,

shelter-seeking and eliminative types of social behaviour.

Although this classifactory scheme is widely recognized by

behavioural scientists, one major shortcoming is that it fails to

recognize several important social relationships of the inter-specific

type. Scott acknowledges only the intra-specific type; i.e. between

the same species. He may account for this by the added clause in

his definition, "usually between the same species", but this still

does not negate the fact that different species often interact in

regular and predictable ways. For example, symbiosis, commensalism

and parasitism are widespread occurrences in the animal kingdom, but

of more importance, for the concern of this treatise at least, Scott

fails to mention the inter-specific social relationship between

predator and prey.

Initially this exclusion may be overlooked for one probably

would not regard this type of relationship as social in the first

place. Superficially it is difficult to conceptualize how the

destruction of one animal species by another could be regarded as

social and, in fact, it has even been referred to as 'anti-social'

(Kuo, 1960, p-211). Nonetheless, a similar conceptual problem presents

itself when one talks of intra-specific fighting, a social relationship,

which like predation, involves conflict between individuals - although

the conflict in this case being between members of the same species.

However, such conflict on the intra-specific level is usually treated

as a kind of social behaviour (Dimond, 1970; Tinbergen, 1953) and

likewise these authors also treat predation, or inter-species conflict,

in the same manner. The basic reason for this is that both of these

interactions are based on regular and predictable behaviours; hence

each must be regarded as a type of social relationship. Further, it

should be realized that both predator and prey reciprocally influence

the other's behaviour and on these grounds alone the relationship

qualifies as something which is social. For example, it is known

that a wide range of predatory mammals have developed through learning

or evolved through natural selection highly specialized behaviours

to capture and kill certain types of prey. Likewise, species that

are preyed upon have acquired their own behavioural and non-behavioural

techniques to avoid capture by their enemies - some of which will be

discussed at a later point in this chapter.

Thus, it would be reasonable to conclude that the predator -

prey interaction is one type of social relationship, and one based

on several regular and predictable types of social behaviour. For

the purposes of our discussion predation in the individual will be

defined as behaviour associated with the capture and consumption of

one animal species by another. The behaviour of the predator can be

broken down into the following three basic components: 1) search

for and approach to the prey; 2) capture and killing and 3) consump-

tion of the prey. The first component, prey search and approach, are

synonymous with Scott's investigative type of social behaviour. The

second component, capture and killing, involves conflict between two

species, hence is synonymous with the agonistic type of social

behaviour. And the last component, consumption, is an ingestive type

of behaviour for it involves eating.

2.2.   BEHAVIOURAL VERSUS NON-BEHAVIOURAL APPROACHES TO THE
PREDATOR-PREY INTERACTION.

Now this social relationship between predator and prey has been

studied from several different vantage points by scientists in a

number of different disciplines. Very generally, those scientists

who fall under the heading of biologists, which may include ornithol-

ogists, zoologists and ecologists, have tackled the predator - prey

interaction on a dynamic level, studying typically not the behaviour

of the individual predator or prey but rather the consequences this

interaction has on the species as a whole. Such workers concern

themselves primarily with non-behavioural topics such as structural

adaption, biotic communities, food chains, animal populations and

species nomenclature. A typical problem which these investigators

would address themselves to would be, for example, how predation by

birds affects the population density of a species of insect or the

functional significance of a particular structural feature which a

species possesses.

On the other hand, psychologists and behaviourally orientated zoologists, such as ethologists, have concentrated on the behaviour of the individual, whether it be predator or prey. This approach is primarily concerned with discerning how exactly prey-capture or predator avoidance develops or is maintained within the individual. A typical problem that would be tackled from this point of view would be, for example, the effects of experience on mouse-killing by rats or the sign stimuli necessary to elicit avoidance in a newly hatched chick.

Although a dichotomy in a general sense should be recognised, one must realize that at best such a dichotomy is not absolute. That is to say, some overlap exists between the various workers in the different fields. So it would be expected to find non-behaviourally orientated biologists tackling behavioural topics and conversely some behaviourally orientated workers tackling non-behavioural topics. An example of the former could be found in Wickler (1968) who discusses how structural adaptions may be behaviourally employed in predator defence and an example of the latter could be found in the researches of Kruuk (1969, 1972a) who has attempted to relate predator - prey interactions to such matters as population dynamics and species ecology.

In summary, then, two basic approaches can be distinguished in the study of the predator - prey social relationship. The first, a non-behavioural approach, has been largely adopted by biologists and the second, a behavioural approach, has been mainly taken up by

ethologists and psychologists. Each of these approaches will now

be discussed.

2.3.   THE NON-BEHAVIOURAL APPROACH.

First, biologists have shown interest in the fact that many

species have adapted structurally to aid their predatory behaviour.

One only needs to look at the large canines of some of the carnivores

and this would immediately become apparent. The teeth of some

insectivores are also adapted to suit their food habits. For example,

the pointed cusps on the cheek teeth of some species make them suitable

for holding and chewing hard coated insects. Likewise the beaks of

birds and the snouts of some fish have also become specially adapted

to assist in the procurement of food.

Species that are preyed upon have also evolved structural means

to ward off predators. The spines of the stickleback serve this

function (Hoogland, Morris and Tinbergen, 1957) and the spines of some

mammals, such as the porcupine and hedgehog, obviously serve a simi-

lar function. No doubt the hard shells of some species, like turtles

and clams, also provide protection from predators. Camouflage is

another non-behavioural recourse that has been taken by some prey.

The resemblance of a species colour or structure to match the environ-

ment is widespread throughout the animal kingdom. The stick insect,

the cryptic colouring of some fish and the stripes of the zebra are

some common examples. It is also of interest to know that some species

have structural features which serve to divert the attack of a predator

to a less vulnerable part of the body. Ross (1965), for example,

cites the appropriate named two-faced fulgoid beetle, found in Asia,

whose posterior is usually mistaken for the anterior by most predators;

hence when a predator strikes damage to the beetle's more vulnerable

parts is avoided. Other fascinating examples of specialised struct-

ural adaptions for defensive behaviour can be found in Eibl-Eibesfeldt

(1970) and Johnson (1972).

Second, biologists have shown interest in the non-behavioural

aspects of the predator - prey relationship because of the belief that

the population size of a prey species is regulated through the preda-

tory behaviour of a different species with which it shares its habitat.

For example, it is believed that when the numbers of a particular prey

population increase beyond a certain limit, so as to become surplus,

then the population becomes more susceptible to predation. Eventually

such predation serves to bring the prey population back to an optimal

level (Cloudsley - Thompson, 1965, p-42). That is to say, when a

population of prey over-saturates the particular niche in which it

lives then predation will start to act as a population regulatory

mechanism. Predation along with starvation and disease are referred

to as 'density dependent variables' (Wynn-Edwards, 1962). But, more

often than not, a population of prey and predators who share the same

niche usually maintain themselves in a constant ratio year in and

year out. Elaborate food chains, food webs and food pyramids have

been hypothesised to account for this phenomenon of ratio consistancy.

The zoologist Weisz (Weisz, 1968) in his text writes,

"Food pyramids are one of the most potent factors in
maintaining communal steady states; significant vari-
ations of numbers at any level of a pyramid soon bring
about automatic adjustments at every other level. For
example, an overpopulation of carnivores might result
in the depletion of herbivores, since a greater number
of herbivores is eaten. This depletion might lead to
starvation of carnivores, hence to a reduction of their
numbers. Underpopulation of carnivores then could
result in overpopulation of herbivores, since fewer
herbivores are eaten. But the fewer carnivores could
be well fed. They might therefore reproduce relatively
rapidly, although the numbers of all kinds of organisms
would undergo short-term fluctuations, the total quan-
tities could remain relatively constant over the long
term" (p-241).

Directly related to this notion of population density is the

concept of _search_ _image_ initially proposed by L. Tinbergen (Tinbergen,

1960 as reported in Marler and Hamilton, 1966). What Tinbergen dis-

covered was that certain birds, such as great tits, selected prey

according to the density of the various prey populations in their

habitat. For example, when a new prey species appeared in the tits

habitat (usually an insect) it was not immediately taken as prey

but rather the tits waited until the population reached a certain

density and only then was it exploited as a source of food. Thus,

Tinbergen believed that when a prey species became relatively abundant,

a tit would then develop a specific search image for that type of

prey. In connection with this finding, Holling (1959) found that the

number of sawfly cocoons eaten by mice and shrews were by no means

random but fluctuated directly with the density of the cocoons; at

low densities these predators took fewer cocoons than when the densit-

ies were at a higher level. Thus, there is evidence for the existence

of a search image within a mammalian species.

Finally, one last reason why biologists have concerned themselves

with the predator - prey relationship rests in their attempts to

systematize animals according to the foods they consume, hence their

interests in who eats who. A species is said to be carnivorous if

it is largely a meat eater, herbivorous if it is a plant eater,

omnivorous if its diet consists of a wide range of edible substances,

insectivorous if it feeds largely on insects, granivorous if it feeds

on seeds and pisciverous if it is a fish eater. Some species common

names are derived from the species they prey upon; for example, the

spiny ant eater, the grasshopper mouse, the fishing cat, the fishing

bat and the crab-eating fox.

Concluding it should be said that the purpose of this section

was to simply give a cursory sketch, along with examples, of some

typical problems the biologist confronts himself with when studying

the predator - prey interaction from a non-behavioural point of view.

The interested reader should consult the classic text of Allee, Emerson,

Park, Park and Schmidt (1949) or Klopfer (1962) for a comprehensive

review of some of the topics that were discussed.

2.4.   THE BEHAVIOURAL APPROACH.

As mentioned earlier it has been mainly psychologists and ethol-

ogists who have tackled the predator - prey interaction with a

behavioural approach. Basically the interest of these workers lies

in the behaviour of the individual predator or prey; rarely does their

research touch on such non-behavioural topics as structural adaption,

nomenclature or population dynamics. The research of these behaviourally orientated workers will be the topic of discussion for the remainder of this chapter and it will be presented in two sections. The first will be concerned with the behaviour of the prey. This will be very short when compared to the second more comprehensive review which will concern itself with the behaviour of the predator. The difference for the amount of material to be covered rests on the fact that the experiments to be subsequently reported in this treatise deal solely with the predatory behaviour of a small rodent, the golden hamster; hence, any background material should logically be drawn from studies dealing with the behaviour of other predators and especially mammalian predators. However, due to the social nature of the interaction between predator and prey it would be best to get at least a rough idea of how the prey behaves when confronted with a predator. Therefore, we will now briefly concern ourselves with this topic.

2.4a   The Behaviour of the Prey.

The behaviour of all prey is naturally concerned with avoiding capture. Such avoidance behaviour is commonly referred to as 'anti-predator' behaviour or 'defensive' behaviour and it occurs on both the individual and communal level. Communally, the schooling of fish or the flocking of birds can be viewed as behaviour concerned with protecting the individual against predatory attack. Obviously a solitary animal is more vulnerable to attack than one which is in a group. Moreover, it is known that predators find it perceptually confusing to single out an individual animal from a group and, in fact, the

strategy of some predators when they come up against an aggregate of

potential prey is to isolate a particular individual and concentrate

solely on it for the kill (Tinbergen, 1951). In addition to grouping

as a means of defence some species 'mob' together to chase off their

adversaries. Hinde (1954) in a widely read paper has described the

mobbing of chaffinches towards owls. Communal defence against pred-

ators can also be seen in some species of antelope. If, for example,

an individual within a grazing herd detects the presence of a predator

it will immediately erect the white hair on its rump and this in turn

provides a signal to the rest of the members of possible predatory

danger (Etkin, 1964). Other interesting examples of communal defence

by prey against predators can be found in Marler and Hamilton (1966)

or Eibl-Eibesfeldt (1970).

On the individual levels animals have adjusted behaviourally

to prevent capture. Activity cycles, the ability to hide, freezing,

protean display, tonic immobility and rapid withdrawal are examples

of some gross behavioural adaptions taken by prey. Noxious deterents

are also used widely by some species. For example, many insects are

known to be highly noxious in taste to some birds and some even

derive their noxious substances from the plants they feed on (Brower

and Brower, 1964). Other species, such as skunks and snakes, depend

on noxious chemical substances to deter their enemies (Whittaker and

Feeny, 1971). Often, as in the case of skunks, an animal possesses

a discrete behaviour enabling it to spray the chemical directly onto

the predator. Another means by which some prey deter predators is by

changing their appearance. For example, this seems to be the function

of eyespots which are found on the hindwings of some moths; when suddenly displayed they are effective in chasing off predacious birds (Blest, 1957).

Much of the defensive behaviour of prey involves the principles of mimicry. Mimicry is usually regarded as the imitation in form, colour or behaviour by a comparatively defenceless and palatable species (mimic) of another more dangerous and unpalatable species (model), the latter of which has the qualities that cause it to be avoided by predatory animals. More simply stated, some prey species gain protection from predators by imitating or mimicing the characteristics of a more dangerous species. Take, for example, the case of several species of darkline beetle found in the southwest United States. One species of this beetle defends itself from predatory attack by standing on its head and spraying an irritating substance from its abdomen. Another closely related species which lives in the same region also stands on its head when threatened although it does not have the defensive secretion (Eisner and Meinwald, 1966). Thus, the latter gains protection by mimicing the behaviour of the former. Many other interesting examples along with a discussion of the evolution of such displays can be found in Wickler (1968).

Some of the better known experiments concerned with anti-predator behaviour have been conducted jointly by the two founders of modern ethology, K. Lorenz and N. Tinbergen (reported in Tinbergen, 1951). Lorenz and Tinbergen examined the alarm response (e.g. crouching and emitting calls) game birds and geese showed to cardboard silhouettes

of birds which were 'flown' above their pens on a wire. They found
that the models most effective in eliciting the alarm response had
the common feature of a short neck which, as they knew, was charac-
teristic of most birds of prey. In one experiment they used a
silhouette which had the effect of simulating a hawk if flown in
one direction and a goose if flown in the opposite direction and,
as expected, their test birds responded with more alarm to the hawk
than to the goose. Lorenz and Tinbergen explained this result in
terms of an innate releasing mechanism responsive to bird species
with a short neck moving in a certain direction.

Unfortunately this experiment, as Manning (1967, pp. 51 - 52)
points out, is open to a number of serious criticisms. First, Lorenz
and Tinbergen tested only adult birds; hence their subjects could
have learned previously what hawks looked like. Second, these authors
scored only the reaction of the group as a whole; thus the reaction
of individuals could have varied and further an individual's reaction
could have been influenced by the behaviour of its pen mates.

Several investigators have attempted to repeat this experiment
under more controlled conditions and on the whole the results have
failed to confirm the original findings. For example, Hirsch, Lindley
and Tolman (1955) tested naive leghorn chicks individually and found
no greater alarm to the hawk than to the goose. Schleidt (reported
in Manning, 1967) working with turkeys found that the alarm response
could be released to a number of models of almost any shape provided
they moved at a certain speed. On the other hand some support for

Lorenz and Tinbergen's original findings have come from the research of Melzack, Penick and Beckett (1959).- Like Lorenz and Tinbergen these authors also found that naive ducklings would respond with more alarm to a hawk than a goose; however, they also found that the birds rapidly habituated to each of the models so that they eventually stopped responding with fear altogether.

No further discussion of the behaviour of the prey will be presented. Hopefully this short review will have provided the reader with a feeling for the topic of anti-predator behaviour; for a more elaborate treatment one should consult Marler and Hamilton (1966), Eibl-Eibesfeldt (1970) or Maier and Maier (1970).

2.4b.   The Behaviour of the Predator.

Predatory behaviour has been studied in a wide range of species which include fish (Beukema, 1968; Chiszar and Windell, 1973; Foxx, 1972; Markl, 1972; Tugendhat, 1960), birds (Mueller, 1973; Mueller and Berger, 1970; Payne, 1961; Orians, 1969; Smith, 1973), insects (Etienne and Howland, 1964; Gardner, 1964; Rilling, Mittelstaedt and Roeder, 1959; Wharton and Arlian, 1972), reptiles (Burghardt, 1964, 1967, 1969; Burghardt and Abeshaheen, 1971; Loop and Bailey, 1972) and amphibians (Eibl-Eibesfeldt, 1952; Ewert, 1970; Ingle, 1973a, 1973b, 1973c). This list could certainly be extended for one gets the impression after reviewing the literature that virtually every type of animal species captures and eats another type of animal species for feeding purposes to some extent. Such a list might begin with the

relatively simple protozoan <u>Deleptus</u> (Brown and Jenkins, 1962) and

continue all the way up the phylogenetic scale to the complicated

chimpanzee (Goodall, 1963; Teleki, 1973; also see Bygott, 1972).

In fact, since predation is so widespread, Cloudsley-Thompson asserts

that it is a "universal phenomenon throughout the animal kingdom"

(1965, p-39). For this reason the amount of literature on the behav-

iour of the predator is expectedly enormous and any attempted review

could well fill a large sized volume. Perhaps this is the reason why

no such review is available, however, a recent review on carnivore

predation can be found in Ewer (1973) and a short review of mammalian

predatory behaviour in general can be found in an earlier publication

by the same author (Ewer, 1968a). A review of the predatory behaviour

in some of the commonly studied mammalian species will now be presented.

This review should enable the reader to gain a perspective on the work

that has been done in the field as well as providing a background with

which to approach the experiments to be subsequently reported in this

treatise.

Before proceeding with a discussion about predatory behaviour

per se mention should be made of a semantic controversy which has

cropped up among researchers during the last few years. What seems

to have happened is that ethologists and psychologists have come to

use different terms when referring to this interaction between

predator and prey. Ethologists, on the whole, when examining this

interaction have always tended to look at all three components of the

predacious act; i.e. search, capture and kill, and eat. Generally,

they conceive the behaviour as a food getting response and in most

text-books written from an ethological orientation the behaviour is
treated under a section dealing with food procurement (Eibl-Eibesfeldt,
1970; Ewer, 1968a, 1973; Maier and Maier, 1970). On the other hand,
psychologists have tended to regard this behaviour as a kind of aggres-
sion (Clark, 1962a, 1962b; Dimond, 1972; Moyer, 1968) and have
labelled it with such names as interspecies aggression (Baenninger
and Ulm, 1969), predatory aggression (Moyer, 1968), killing behaviour
(Karli, 1956) and muricidal behaviour (Kulkarni, 1968b; Miczek and
Grosman, 1972). This attitude is perhaps best reflected in the words
of Thomas (1971), a psychologist,who describes the predatory behaviour
of the domestic mouse as being "aggressive in general nature, for
the mouse must ...... attack it and immobilise it somehow" (p-1).

The reason for this difference probably lies in the fact that
psychologists have tended to look only at the middle part of the
predatory sequence, i.e. capture and kill, and ignore what normally
precedes it, i.e. the search, or what normally follows, i.e. consump-
tion. In fact, in a number of studies, particularly those of Myer
(1964, 1969, 1971), the prey is usually removed shortly after the
kill. The reason why psychologists treat this behaviour as a kind
of aggression is probably because the part of the sequence they do
study (the capture and kill) does involve conflict. Observation of
both inter- and intraspecies conflict shows that often similar behav-
ioural patterns are involved (Baenninger and Baenninger, 1970; Thomas,
1972). For example, rats and mice use both their teeth and paws in the
capture of prey and when fighting conspecifics. Moreover, another
reason for this difference between psychologists and ethologists could

stem from the zeitgeist or 'spirit of the times'. Currently, it could be argued, that due to the increased turmoil and violence within western society pressure has come to bear on both animal and human researchers (perhaps from government agencies who finance research projects) to provide explanations for society's disquiet. Thus, psychologists have probably become prone to label any behaviour which closely resembles what traditionally has been regarded as aggression, i.e. fighting between conspecifics, as a kind of aggression. Whether predatory behaviour is a kind of aggression is largely a semantic debate. If it be defined as the capture and consumption of one animal species by another then strictly speaking it is not. However, Moyer (1968) has cogently argued that in some instances it may be treated as such.

2.4b.1. Species of Investigation.

By far the most intensively and extensively investigated predator has been the domestic variety of Rattus norvegicus, more commonly known as the white rat or laboratory rat. In fact, the majority of scientific publications since 1960 which have been concerned with the predatory behaviour of a mammal have been about the white rat. Karli (1956) was the first to report on the predatory behaviour of this species and subsequent experimentation has been most notably carried out by James Myer and his students (for example see Myer, 1964, 1966, 1967, 1968, 1969, 1971; Myer and White, 1965; Van Hemel and Myer, 1970). Some information on the wild form of Rattus norvegicus was also reported by Karli (1956) and later by both Eibl-Eibesfeldt (1958) and Galef (1970), and Ewer (1971) has reported some observations on the related

<u>Rattus</u> <u>rattus</u>. Other rodents which have been studied in the laboratory include the wild and domestic forms of <u>Mus</u> <u>musculus</u> (Thomas, 1969, 1972), the deer mouse (Thomas and Fried, 1971), the northern grasshopper mouse (Boice and Schmeck, 1968; Clark, 1962a) and southern grasshopper mouse (Thomas and Fried, 1971).

Next to the order Rodentia the order Carnivora has been most thoroughly studied. Many of these studies have taken place in the field; for instance, in the national parks on the African continent or in semi-natural conditions like zoos. The large feral cats of the felid family have been studied in this way (for example, see Eloff, 1964, or Kruuk and Turner, 1967). The recently published field studies by Kruuk (1972a) and Schaller (1972) have substantially increased our knowledge about the predatory habits of hyaenas and lions. The predatory behaviour of the African hunting dog has also been the subject of several field investigations (see Estes and Goddard, 1967, or Kuhme, 1965). In the laboratory other species of the canid family, such as the fox, wolf, coyote and dog have been subject of some inquiries (see Kuo, 1967 for a summary of his studies, and Fox, 1971 for a summary of his studies). The classic studies of Kuo (1930, 1938) and Leyhausen (1956) have revealed much about the predatory behaviour of the common household cat; excluding the domestic rat, the domestic cat has been the most thoroughly studied predator. Other carnivores that have been studied include species from the felid family (Leyhausen, 1973), mustelid family (Eibl-Eibesfeldt, 1961, 1963; Gossow, 1970 for the polecat; Wustehube, 1960 for polecats, weasels and stoats; Hall and Schaller, 1964 for the sea otter) and viverrid family (Rasa, 1973 for the dwarf mongoose; Ewer, 1963 for the meerkat; Eisenberg and Leyhausen, 1972

for several species). Other mammalian orders that have been studied

include Marsupialia (Ewer, 1968b for the marsupial mouse; Ewer, 1969

for the mulgara and Tasmanian devil; Roberts, Steinberg and Means,

1967 for the opossum), Chiroptera (Griffen, Webster and Michael, 1960,

and Webster and Griffen, 1962 for bats) and Insectivora (Rood, 1958

Blossom, 1932 for the shrew; Eisenberg and Gould, 1966 for several

species).

The kind of prey that has been offered to laboratory predators

has varied but in the majority of studies domestic mice have been

used. For example, Myer and Karli in all of their experiments have

exclusively used mice. Karli (1956) states that one reason he chose

to study the rat - mouse interaction was because "the conflict rat

vs. mouse is not an artificial situation created by the experimenter

but a biological phenomenon observed in nature" (p-82). In addition

to mice, frogs have recently been increasingly used as the subjects

of prey (for example, see DeSisto and Huston, 1970, 1971, or Kilbey,

Moore and Harris, 1973). Other species which have been presented to

rats include chicks and turtles (Bandler and Moyer, 1970; McDonough,

Manning and Elsmore, 1972)and cockroaches (Johnson, DeSisto and

Koenig, 1970, 1972). In the investigations in which mice served as

predators (Thomas, 1969, 1971, 1972) crickets were offered. In the

studies with grasshopper mice the prey offered them have included

domestic mice, crickets, scorpions, crayfish, salamanders, lizards

and frogs (Horner, Taylor and Padykula, 1965). Horner et al. stressed

the fact that scorpions were a 'natural' prey object for Onychomys.

In the studies in which domestic cats have been used mice and rats

have usually served as prey. However, in one study Kuo (1960)

offered his cats a wide range of prey which included rabbits, rats,

guinea pigs, canaries, sparrows and parrots.

The ethologist, Ewer (1969), classified the prey she offered

to her marsupial predators into four basic types (for reasons to

be explained later); these included: 1) small innocuous inverte-

brates (mealworms, crickets and grasshoppers); 2) larger inverte-

brates not overpowered by a single bite and capable of fighting back;

3) snakes and small lizards and 4) larger vertebrates, such as mice.

In similar fashion, Eisenberg and Leyhausen (1972) classified the

prey which they offered to several species of Carnivora and Insectivora

into two distinct types: Class 1, which included innocuous prey

incapable of defence (chicks and mice) and Class 2, which included

prey capable of defending themselves (hamsters and rats).

In the wild the investigator has little or no control over the

prey which a predator might take, hence the most that can be done is

simply to note what species a predator preys upon. Kruuk (1972b),

for example, reported that several species of large feral carnivores

took mainly Thomson's gazelle, zebra and wildebeest in a national

park in Africa. Ewer (1971) studying feral <u>Rattus</u> <u>rattus</u> in their

natural habitat noted that they preyed upon termites, moths, dragon-

flies, toads and mice.

2.4b.2. Methods of Investigation.

The ethologist, who typically conducts most of his research in

the field, faces the initial task of locating the predator in its

natural habitat. This might not be as easy as it might initially

seem for many of the large predatory cats are close to becoming

extinct, hence locating them could well present problems. This

could be the reason why only one published account on the predatory

behaviour of the highly carnivorous tiger (Panthera tigris) exists

(Schaller, 1967) and the number of other studies on the large feral

cats are surprisingly few. Predators captive; in zoos have provided

some opportunity for ethologists to observe their behaviour under

more or less semi-natural conditions. However, the number of preda-

tors available for study under these conditions are often limited so

consequently much of the research that has come out of the zoo studies

has been largely concerned with filming the behaviour of just a few

animals and then meticulously describing it. This is the approach

Eisenberg and Leyhausen (1972) took in their study which lasted several

years. Ewer's (1968b, 1969) observations on marsupials, which she

studied in large outdoor pens, epitomizes the traditional ethological

approach; i.e. small sample size studied under 'natural' conditions

with a heavy emphasis on description.

The approach of the psychologist, on the other hand, has been

to test a fairly large number of subjects in the controlled conditions

of the laboratory. Testing is usually carried out in a subject's own

home cage or in a novel test cage to which it was allowed to acclimatize.

The prey is usually introduced through a trap door or dropped in through

the cage top. Once exposed to the prey subjects have been allowed

various times, arbitrarily set by the experimenter, in which to make

a capture and kill. For example, Korn and Moyer (1968) allowed two

minutes, Miley and Baenninger (1972) five minutes, DeSisto and Huston

(1970) ten minutes, Ueki, Fujiwara and Ogawa (1972) fifteen minutes,

Johnson, De Sisto and Huston (1970) twenty minutes, Thomas (1969)

thirty minutes, Flandera and Novakova (1971) one hour, Myer (1971)

two hours, Bugbee and Eichelman (1972) eight hours, Eichelman, DeJohn

and Williams (1973) twenty-four hours, Bandler and Moyer (1970)

forty-eight hours and Spector and Hull (1972) one week. Sessions are

terminated after the time has elapsed (at which time the prey is

removed), or when the subject has made the kill. In a few experiments

subjects have been permitted to feed on the prey (Bandler and Moyer,

1970; Kuo, 1930; Karli, 1956; Paul, 1972: Paul and Posner, 1973;

Thomas, 1969) but in the majority of studies the prey has usually been

removed shortly after the kill. In some experiments subjects have been

given just a single test (Denenberg, Paschke and Zarrow, 1968; Galef,

1970) while in others several successive tests have been administered

(DeSisto and Huston, 1970; King and Hoebel, 1968; Lonowski, Levitt

and Larson, 1973; Panksepp, 1971c; Panksepp and Trowill, 1969;

Thomas, 1969). Another procedure which has been widely used has been

to test only those subjects who had been previously screened out on

the basis of some criterion. For example, Myer in several of his

studies (see Myer, 1964, 1967, 1968) started with a group of naive

subjects and tested them until they met the criterion of killing or

failing to kill on ten successive tests. Subjects who met the

criterion of killing were then selected out for further study and those

who met the non-killing criterion were discarded.

The measures taken in most laboratory investigations have been latency to attack(Miley and Baenninger (1972) define it as the stereo-typed, co-ordinated response in which the rat seizes the mouse with its forepaws and bites into it with downward head motions directed mainly at the mouse's dorsal surface;   for the mouse, Thomas (1972) defines it as the "pouncing on the cricket and tearing at it with the forepaws or biting it, or both" (p-2)), latency to kill (defined by Baenninger, 1967, as the cessation of all movements of the prey, or as the permanent immobilization of the prey, as defined by Relvis and Moyer, 1969) and occasionally latency to eat.   In other studies investigators have rated the behaviour of the predator on scales ranging from tolerant (of the prey) to hostile (Kuo, 1930), or from indifference to overt attack (Kuo, 1960).   Still other investigators have made use of the multiple pen recorder which enabled them to record several behaviours, such as nips, explorations and other behaviours related to prey killing, simultaneously (Thomas, 1969, 1972; DeSisto and Huston, 1970).

2.4b.3.   Basic Behavioural Patterns.

The predatory behaviour of most mammals can be conceived as being organised into the following three components:

1) Search for and approach to the prey.

2) Capture and killing.

3) Consumption of the prey.

Search and approach: Search is usually the behaviour which

initiates the predatory sequence.   In the case of a search or a hunt

(these two words may be used interchangeably) the predator does not

have cognizance of the location of the prey but is actively seeking

it via its exploratory behaviour.   The search may involve a journey

of several miles or it may hardly involve any movement at all.   For

example, the searching behaviour of the African hunting dog often

covers several miles (Kuhme, 1965), while on the other hand, predators

like marsupial mice often just sit motionless in their territory on

the alert for prey (Ewer, 1968b).   The search component may also take

the form of vigorous digging behaviour (Ewer, 1963 for observations on

the meerkat;   Eisenberg and Gould, 1966 for several insectivores) which

functions to unearth small prey concealed in crevices, or it may take

the form of rapid movement with the vibrissae accompanied by locomotor

movement (Thomas, 1969).   Laboratory rats and mice typically search

in this manner.   Perhaps the most highly specialised type of searching

behaviour can be found in the insectivorous bats who emit ultrasonic

pulses in their attempts to locate prey (Griffen, Webster and Michael,

1960).

Once the prey is located the next behaviour in the predatory

sequence is that of approach.   By far the most elaborate kind of

approach can be found in certain felid species.   Take, for example,

the approach behaviour of the domestic cat which Ewer (1968a) lucidly

describes:

"Cats stalk their prey by using a series of distinctive
movements. When first alerted to the pressence of the prey
at some distance, the cat crouches and then hurries towards
it with the body flat to the ground in what Leyhausen calls
the slink-run. At a distance determined by the available
cover she pauses and 'ambushes', crouched low with the whole
of the sole of the foot on the ground and the forepaws sup-
porting the body directly under the shoulders, the whiskers
spread and the ears turned forward. For a few moments she
watches the prey, her head turning as she follows its every
movement, as though her eyes were tied to it by an invisible
cord. Depending on the distance and cover, a second slink-
run and ambush may follow and cautiously, to the last piece
of available cover and her again she ambushes and prepares
for the kill" (p-35).

This type of slow and deliberate stalking approach has been

found to occur in a number of other species besides those of the

felid family. For example, it has been observed in several species

of Canidae (Fox, 1969, 1971; Kuhme, 1965), in a marsupial species

(Eisenberg and Leyhausen, 1972 for the marsupial mouse[1]) and it has

been reported that it even occurs in a rodent species, the grasshopper

mouse (Boice and Schmeck, 1968; Clark, 1962a). In connection with

this latter finding, it should be noted that no investigator has

ever reported any sort of stalking behaviour in the most commonly

studied predator, the white rat.

Capture and kill: Once the prey is located and subsequently

approached then the capture will be attempted. The capture phase

of the predatory sequence may be regarded as behaviour associated

with positioning the prey so that the behaviour subsequent to it,

---

1. Whether or not the marsupial mouse stalks prey is a matter of
controversy. Ewer's (1969) observations led her to conclude
that this species lacked the typical stalking approach.

that of killing, can be made with relative ease. This can occur

in a number of ways. Domestic cats spring into the air and seize

the prey with their forepaws (Leyhausen, 1956, reported in Ewer, 1968a).

Large feral cats simply knock the prey over by hurling their body

through the air or by swatting it with their forepaws (Eloff, 1964).

Domestic rats make the capture by seizing the prey with their forepaws

(Baenninger, 1967). Certain mustelid species, such as weasels and

stoats, seize the prey initially with their mouth (Gossow, 1970).

Several insectivores and carnivores often use both their paws and

mouth in combination to assist in capture (Eisenberg and Leyhausen,

1972).

Once captured a good number of predators will take the prey

in their mouths and shake it violently from side to side. This type

of behaviour has been referred to as the 'death shake' (Ewer, 1968a;

Leyhausen, 1973) and it has been observed in marsupials (Ewer, 1968b,

1969), canids (Fox, 1969, 1971), viverrids (Eisenberg and Leyhausen,

1972), insectivores (Herter, 1957; Lindemann, 1951; Rahm, 1961,

all reported in Ewer, 1968a). Fox (1971) asserts that the death shake

in Canidae serves two functions; namely, 1) to prevent the prey from

striking back and 2) to crush the prey to death. Ewer (1968a) is in

basic agreement for she postulates that the death shake acts to upset

the labyrinthine reflexes of the prey, thus reducing its ability to

resist. Interestingly enough, Ewer also notes that most species of

felid lack the typical death shake. She reckons that this is due to

the development of their highly effective canine teeth along with

their accurately orientated killing bite. According to Ewer.the death

shake is both unnecessary and disadvantageous for species within this family for if it did occur it would probably interfere with the typical method of killing; i.e. by inserting the canine teeth into the nape of the prey's neck (see below). Lastly, it should be mentioned that no one has ever reported any behaviour resembling the death shake in the domestic rat, or for that matter any other rodent species.

Killing in a wide range of species is often accomplished with a bite directed towards the nape of the prey's neck. Even the domestic rat kills in this fashion (Bandler and Moyer, 1970; Karli, 1956; Myer, 1964 and many others). When a predator bites into the nape of the prey's neck its teeth cut through the cervical spinal chord and/or hind brain with death occurring almost instantaneously (Ewer, 1968a; Leyhausen, 1973). Other Carnivora which kill with the neck bite include most species of Felidae (Leyhausen, 1973) and several species of Viverridae (Eisenberg and Leyhausen, 1972). Most species of Mustelidae also kill with a neck bite (Eibl-Eibesfeldt, 1961, 1963; Gossow, 1970; Wustehube, 1960). Some insectivores, such as shrews (Heptner, 1939 and Herter, 1957, both cited in Ewer, 1968a) and some marsupials, such as the Tasmanian devil and mulgara (Ewer, 1969), likewise kill with a bite to the neck of the prey. Those predators which do not kill with a neck bite (usually pack hunting predators such as hunting dogs, wolves and related canids) usually suffocate the prey to death, strangle it, crush it with their teeth, or kill it with an accumulation of minor unorientated bites (Allen and Mech, 1963; Fox, 1969).

Consumption: The last stage of the predatory sequence is con-
cerned with eating the prey which the predator has killed. Both
Karli (1956) and Paul and Posner (1973) found that domestic rats
preferred to eat the brain of a mouse; wild rats, on the other
hand, showed no such preference; they usually start eating at the
point where they made the kill (Karli, 1956). Rood (1958) also
reported that short-tail shrews preferred the brain of a mouse.
Bandler and Moyer (1970) note that the rats which killed turtles
often pulled the head of the turtle from the shell in order to eat
it. These authors also found that rats which killed frogs usually
began to feed initially on the frog's legs. Likewise, mice which
kill crickets will occasionally commence eating from the legs
(Thomas and Fried, 1971). In several carnivores, and in some mar-
supials, there is a strong tendency to begin eating the prey from
the anterior end and continuing downwards. The domestic cat always
eats a mouse from the head down and even a young kitten given the prey
which itself has not killed will eat in this fashion (Leyhausen, 1956
reported in Ewer, 1968a). Other Carnivora, such as viverrids and
mustelids and one species of Rodentia (the grasshopper mouse) also
show a strong inclination to eat the prey from the head down (Ewer,
1968a; Thomas and Fried, 1971). On the other hand, predators which
hunt in packs show no specific eating orientation. Usually predators
which kill communally, feed communally, hence animals within a pack
usually begin to feed simultaneously from a number of different spots
(Estes and Goddard, 1967).

Lastly, before this section on basic behavioural patterns comes

to an end, it should be recalled that both Ewer (1969), and the team

of Eisenberg and Leyhausen (1972), classified the prey they offered

to their predators into several distinct types. These classifica-

tions were necessary because they both observed that the behavioural

patterns their predators employed in capturing prey were strongly

influenced by the characteristics of the prey itself; hence differ-

entation in terms of the kind of prey offered was needed. For example,

Ewer noticed that the differences in the way in which her mulgara

attacked and killed different types of prey were striking. Small

innocuous invertebrates were usually seized without hesitation and

immobilised by a single unorientated bite. They were never shaken.

In contrast to this, the larger invertebrates were usually bitten

several times, violently shaken from side to side and then dropped.

This sequence of bite, shake, drop was repeated as often as required

to immobilise the prey. Snakes and small lizards were likewise

treated with the bite, shake, drop technique. Mice, however, were

treated differently. If they defended themselves when the mulgara

approached they were not initially killed; instead, the mulgara

withdrew and avoided contact. However, with experience, the mulgara

came to kill with a single aimed bite directed to the neck of the

prey. Shaking the prey never occurred.

Eisenberg and Leyhausen also observed differences in the predatory

behaviour of another marsupial, the Virginia opposum, when it was

offered different types of prey. As mentioned earlier, these investig-

ators classified the prey into two distinct types: Class 1, which

included innocuous prey incapable of defence (e.g. chicks and mice) and Class 2, which included prey capable of defending themselves (e.g. hamsters and rats). Now when a mouse was offered to the opposum it was usually killed swiftly with a rapid series of bites delivered to the body. However, when confronted with prey from Class 2 the opposum reacted differently. What it usually did in this situation was to: 1) seize the rat with its mouth, then 2) immediately pin it to the ground with the forepaws, and lastly, deliver bites to the rat's body. Alternatively, it might have: 1) seized the rat with its mouth, 2) shaken it, 3) pinned it to the ground, and then, 4) finally deliver several bites.

The point the reader should grasp from these descriptions, and the descriptions of Ewer, is not particularly the behavioural sequence a predator went through, but rather the fact that a predator did behave differently when confronted with different types of prey. Concerning this point Eisenberg and Leyhausen assert:

> "It should be completely evident through the protocols
> and considering our division of prey objects into
> different classes that the familiarity of the predator
> with the prey and response patterns of the prey itself
> in a large part determine the form of the killing res-
> ponse seen. Prey objects which have the potential to
> injure the predator or somewhat noxious to the predator
> (Class 2)[2] may be treated in quite a different manner
> from objects which are relatively innocuous and are
> easily overcome (Class 1)[2] " (p-87).

Thus, these observations of both Ewer and Eisenberg and Leyhausen

---

2. Author's insertion.

indubitably show that the behaviour of the predator can be influenced by the type of prey it comes up against. The basic behavioural components seem to remain intact; however, as indicated, various vicissitudes may arise within each of these components due to the characteristics of the prey.[3]

In summary, then, three distinct components of predatory behaviour can be identified. The first, search and approach, might be regarded as the appetitive phase of the predatory sequence. The behaviour in this phase, as indicated previously, is usually variable and may be conceived as that which is concerned with searching for and gaining access to a particular goal object, which in this case is the prey. The second phase, capture and kill, might also be regarded as an appetitive link within this behavioural chain for it too is concerned with placing the predator in a favourable position so as to make the goal object more accessible. When the goal object has been obtained, i.e. after it has been captured and killed, the variable behaviour of the appetitive phase gives way to a more fixed and stereotyped response, which is eating, and this might be regarded as the consummatory component. The consummatory component may then give way to a period of quiescence in which the predator is no longer responsive to the stimuli from the goal object and shows no further signs of appetitive behaviour (see Manning, 1967, pp. 56 - 57, for a general discussion on appetitive, consummatory quiescence sequences of behaviour).

---

3. Further these observations buttress the belief concerning the social nature of the predator-prey interaction. As the examples indicate, the prey influences the behaviour of the predator; and vice-versa, the predator influences the behaviour of the prey.

2.4b.4. The Development of Predatory Behaviour.

What factors are responsible for the development of predatory behaviour? To what degree does the predator's nature or nurture determine the mature expression of this response? These are the complex and difficult questions to which we will address ourselves in this section.

Initially, one could easily get the impression that the predatory behaviour of some of the more commonly studied predators, such as rats and cats, universally occurred within these species. That is to say, if given the opportunity in suitable conditions, all rats and all cats would exhibit the predatory response. Certainly popular accounts, like the Disney cartoons, have helped foster such beliefs. However, such beliefs have also been conveyed among scientists themselves for some in the scientific literature have labelled without reservation the rat's or cat's predatory response as something which is innate or instinctive (Horowitz, Ragozzind and Leaf, 1965; Kreiskott, 1969; Kulkarni, 1968a; Myer, 1966; Valzelli, 1967; Yerkes and Bloomfield, 1910). If it is to be regarded as such then what criteria can one adopt to judge whether or not the predatory behaviour of a particular species is in fact an innate, or instinctive, or inborn act?

This issue rests on three questions: namely, 1) can the behaviour be genetically determined, 2) is the behaviour characteristic of the species, and 3) to what extent is the behaviour dependent upon exper-

ience for its development? If the behaviour has a genetic basis

and if it be characteristic of the species and, further develop

fully formed within the individual in the absence of relevant exper-

ience, then may it be regarded as something which is innate?[4] If

so, does the predatory behaviour of the rat or cat or for that matter

any other mammalian predator meet these criteria? The discussion

which follows should enable us to answer these questions.

Question 1: <u>Can the predatory response be genetically determined?</u>

The genetical approach involves two main types of investigation.

Either the researcher can start from a genetically heterogeneous group

and selectively breed in opposite directions for the behaviour in

question, or alternatively he may study different strains of a single

species and look for behavioural differences.

Using the former method Karli, Vergnes and Didiergeorges (1969)

note that they undertook a fairly prolonged breeding programme (two

years) in which they bred male mouse killing rats exclusively with

female mouse killers. Contrary to their expectations this procedure

did not produce a significant change in the spontaneous killing res-

ponse in rats bred for killing; however, it was effective in increasing

the probability of converting a non-killer into a killer by an olfac-

tory deafferentation (this term 'olfactory deafferentation' will crop

---

4. These are essentially the criteria Ewer (1968a) laid down for
    her theory of innateness. This author does not necessarily
    agree with these assumptions but has included them so as to
    make possible the development of the discussion which follows.

up in other parts of this chapter. Most researchers take it to mean
the surgical removal of the olfactory bulbs, or the severing of the
olfactory tracts).

More promising results with the selective breeding technique
have come from the research of Thomas (1972). She claims to have
successfully bred for fast and slow cricket-killing in domestic mice.
This breeding programme merits particular attention because significant
differences in latency to kill were obtained between the slow and the
fast strains after the first generation. Unfortunately, this research
programme happens to be in a preliminary stage for data has been
reported on only two generations; thus nothing very conclusive can
be drawn. However, it will be interesting to find out if further
separation between the strains occurs after, say, six or seven genera-
tions.

Some research has also been conducted with the latter method;
i.e. comparing the predatory tendencies of established strains within
the same species. Flandera and Novakova (1971) reported that they
studied mouse killing in four strains of laboratory rats (the Wistar-
SPF, Wistar-conventional, Long-Evans and Sprauge-Dawley strains) and
found the incidence of killing to be nearly identical under normal
conditions. However, when pregnancy was induced, rats of the Wistar-
SPF strain killed with a significantly greater incidence than rats from
the other three strains (see Section 2.4b.5).

Thomas (1969, 1971, 1972) in another series of experiments with

mice also reported positive results. Again the behaviour looked

at was cricket killing and she found that the males of the two

strains of mice studied differed considerably. The I^S/Crgl strain

proved to be bold and efficient captors and killers when compared

to the C57BL/Crgl strain which behaved with ambivalence and fear

when initially confronted with the prey.

In conclusion, with mice it appears that those genes affecting

the latency of insect capture and killing can be selected out from

naturally occurring variation within a hetergeneous population.

With rats, the evidence at present suggests that genotype probably

has no direct influence, but if combined with some other treatment

as Karli et al. (1969) and Flandera and Novakova (1971) have shown,

it may be of some importance.[5] Additional studies on the genetics

of predation should broaden the range of species under study and

concentrate on genotypical-phenotypical variation, dominant - recessive

relationships between genes, the number of genes in control of the

response, and genotype - environmental interaction.

Question 2: <u>Is predation characteristic of the species?</u>

One of the most salient findings that has emerged from the research

concerned with mouse killing by rats or rat killing by cats is that

not all will kill when given the opportunity. A number of investigat-

ors have reported that only between 10% and 20% of domestic rats

---

5. Also see Paul, Miley and Baenninger (1971) who found hunger-
   induced killing dependent on the strain of the rat being starved.

spontaneously attack and kill mice (Bandler and Moyer, 1970; Karli,

1956; Kreiskott, 1969) and likewise it has been demonstrated by Kuo

(1930) and reported by Flynn, Venegas, Foote and Edwards (1970)

that not all domestic cats spontaneously attack and kill rats. Wild

rats however, are more likely to attack and kill mice; both Galef

(1970) and Karli (1956) report that close to 70% exhibited this

behaviour when tested in the laboratory.

Although most domestic rats will not kill mice, most, however,

will kill frogs. Bandler and Moyer (1970) reported that nearly 100%

of the rats they tested killed frogs. This important finding was

confirmed by DeSisto and Huston (1970) and since then by several others.

Thus, it appears that most rats have within them the capacity to kill,

and whether or not this behaviour is expressed seems to depend largely,

on the characteristics of the prey.

Still more convincing evidence that most rats possess the poten-

tial to kill comes from several neurophysiological studies. For

example, Bandler (1969) and later Smith, King and Hoebel (1970),

screened out and selected for use in their experiments proven non-

mouse killing rats and injected directly into their lateral hypothal-

amus a cholinergic drug known as carbachol. In both experiments it

was found that by chemically stimulating a rat's brain in this way it

was possible to convert rats who were normally non-killers into killers.

In similar fashion those researchers who have electrically stimulated

a rat's brain (for example, Vergnes and Karli, 1970, stimulated portions

of the medial hypothalamus and in an earlier study, Vergnes and Karli,

1969, the anterior hypothalamus. In other studies the lateral

hypothalamus, King and Hoebel, 1968, ventral hypothalamus, Panksepp,

1971a, and anterior lateral hypothalamus, Panksepp and Trowill, 1969,

have been stimulated) have found that non-killers which were normally

indifferent in the presence of the prey would kill if stimulated at

the proper brain site.

In another experiment Vogel and Leaf (1972) studied the effects

of another cholinergic compound called pilocarpine. Established non-

killers were repeatedly administered this drug and these authors

reported that this treatment had the effect of converting all of their

subjects into killers. Thus, they concluded, "all rats possess brain

mechanisms that control predatory attack and killing of mice" (p-424).

A very similar conclusion was voiced by King and Hoebel (1968) in their

study cited above. They wrote "we conclude that an innate mechanism

capable of triggering killing is built into the hypothalamus" (p-176).

Researchers have also transformed non-killers into killers through

the technique of brain ablation. For example, there have been numerous

reports which have shown that anywhere between 40% and 100% of non-

mouse killing rats will kill after bilateral removal of the olfactory

bulbs (Alberts and Friedman, 1972; Bandler and Chi, 1972; Bugbee

and Eichelman, 1972; Karli, Vergnes and Didiergeorges, 1969; Kumadaki,

Hitomi and Kumada, 1967; Malick, 1970; Spector and Hull, 1972); partial

bulbectomy is somewhat effective although nowhere nearly as effective

as total bulbectomy (Bugbee and Eichelman, 1972). Prior to these find-

ings Karli (1956) found that lesions of the frontal lobes induced mouse-

killing in some non-killers. In addition, it has been found that

lesions in the ventromedial hypothalamus produced similar effects

(Malick, 1970; Panksepp, 1971b) and recently Miczek and Grossman

(1972) reported that non-killers would kill if their septal region

was lesioned.

Similar findings to the above have also been reported for the

cat. For example, Wasman and Flynn (1962) along with others

(Hutchinson and Renfrew, 1966; Levison and Flynn, 1965; MacDonnell

and Flynn, 1966; Roberts and Kiss, 1964) have demonstrated that non-

killers will kill in the normal feline manner if stimulated electrically

in the lateral hypothalamus. In fact, in most laboratory investiga-

tions the normal procedure has been to stimulate cats in this area

of the brain (other areas of a non-killer's brain from which attack

can be elicited include the dorsal, ventral and medial hypothalamus,

the midbrain, the thalamus and the stria terminalis) in order to

elicit the predatory response; contrary to popular belief the major-

ity of laboratory cats will not attack and kill without such stimula-

tion. (Flynn, 1967).[6]

In another study with cats Roberts and Berquist (1968) tested

subjects who had either been raised alone or communally with conspec-

ifics. When adult subjects were electrically stimulated at various

points in the hypothalamus and presented a rat. It was found that both

the isolated and socially reared cats attacked and killed with qualit-

atively the same type of response, although the isolates tended to be

somewhat less persistent and vigorous in their attacks. On the basis

6. The fact that both the laboratory cat and laboratory rat show a
   considerably lower incidence of 'spontaneous' killing than their
   feral counterparts suggests that domestication has attenuated this
   behaviour in these species.

of this result Roberts and Berquist concluded that the brain mechan-

isms which controlled the cat's predatory response were "probably

innately organised although they are also modifiable by conditions

during development" (p-590).[7]

In summary, then, in light of the above mentioned findings it

would be reasonable to conclude that most rats and cats possess the

potential to kill, for most, if not all, possess the brain mechanisms

associated with the control of this behaviour. Whether or not this

potential overtly manifests itself in the form of predatory behaviour

probably depends on the type of prey offered as well as the animals

genetic make-up.[8] More importantly, however, the expression of this

behaviour could depend on what the animal experiences during ontogeny.

It is to this important and popular area of research to which we will

now turn our attention.

Question 3:   What role does experience play in the development

          of predatory behaviour?

We are now faced with the more challenging problem of determin-

ing what effect experience has on the development of the predatory

response. If in fact we do establish that experience is necessary for

the development of the behaviour then would it be possible to dismiss

the view that predatory behaviour is an instinct? If the orthodox

---

7.   See Roberts and Kiss (1964, p-192) for a similar conclusion.

8.   The validity of this last point rests on the assumption that
     predation has a genetic basis.

view outlined at the beginning of this section is adhered to then

certainly we are justified in doing so. According to this view if

a behaviour is to be regarded as innate or instinctive then it must

occur fully formed within the individual without the benefit of past

experience. Hence, if we do find that experience is necessary and

therefore conclude that predation has no innate basis are we then

justified in saying that the behaviour is something which is 'learnt'?

To argue along lines like these, that is by dichotomizing preda-

tory behaviour into that which is either innate or learnt, would not

only be misleading but also facile and fallacious for the development

of any complex behaviour whether it be predatory behaviour, agonistic

behaviour, maternal behaviour, sexual behaviour, etc., is the product

of the inextricable interaction between what the animal has experienced

and its own genetic make-up. Such an epigenetic approach to behavioural

development has been repeatedly stressed by most contemporary comparat-

ive psychologists (see Moltz, 1965 for a critical discussion); hence,

recognizing the complexity of the developmental process we would

probably be on safer grounds if we abandoned the question we initially

set out to answer at the beginning of this section (e.g. is predatory

behaviour an instinct?) realizing that predatory behaviour simply can-

not be rigidly dichotomized into that which is innate or not innate

(i.e. learnt).[9]

---

9. According to Denenberg et al. (1968) "rather than use an instinct-
learning classification, we feel that a more fruitful approach to
an understanding of behaviour is within a developmental framework
in which the organism's behaviour at any point in time is viewed
as a function of the animal's accumulated experience as well as
his genetic background" (p-39).

Although this epigenetic approach is now widely accepted, one

must realize that there are still some ethologists who cling passion-

ately to the belief that some predators have innate tendencies or

minute chunks of innate behaviour within their behavioural repertoire.

According to ethological theory these chunks of innate behaviour, or

the innate tendencies, form the basis onto which more complex learnt

behaviour is built.[10] The ethologists do not maintain that experience

is without effect, for they too, like most comparative psychologists,

agree upon the fact that experience acts in subtle ways upon the

animal's genotype; however, while maintaining this position they still

insist on labelling certain features of an individual's predatory res-

ponse as being innate or instinctive (for a good example see Rasa,

1973).

The reason why ethologists continue to employ terms like innate

and instinctive probably stems from the general approach they take to

the study of behaviour. Classical ethology and to a large extent ethol-

ogy as it is practiced today has always laid a heavy emphasis on

behavioural description; hence, no doubt through scrupulous film anal-

ysis ethologists have been able to isolate and identify behaviours

which, apparently to them, are more or less fixed and rigid from their

onset and need little or no experience for their development. Because

of this emphasis one gets the impression that ethologists have largely

abandoned the use of the words innate and instinctive as causal explan-

ations and, instead, have generally come to use these terms on the

10. See Ewer (1968a, Chapter 12) or Eibl-Eibesfeldt (1961) for an
    ethologically biased discussion on the relationship between learnt
    and innate in predatory behaviour and consult Lorenz (1965) for a
    general discussion.

descriptive level. In contrast, comparative psychologists have looked

chiefly at the gross effects certain types of experience have on the

predatory response. These workers have been mainly interested in the

quantitative aspects of this behaviour such as frequency of occurrence

or latency to occurrence. Often in their experiments the principal

question asked is 'prey killed or not killed'. Only on occasion has

the comparative psychologist been interested in the descriptive or

qualitative aspects of the response, hence they have had no need to

recourse to terms like innate or instinctive. This distinction between

comparative psychologists and ethologists is fundamental and should be

kept in mind as one reads through the review which follows.

2.4b.4a. The Effects of Experience Prior to the Test Situation

The effects of social isolation

What effect does early conspecific social contact or lack of such

contact have on the development of the predatory response? Such a

question must be asked for it is well known from many other investiga-

tions with many different species that early social experience can have

profound and lasting effects on many adult behaviours (see Denenberg,

1972, or Newton and Levine, 1968 for a collection of papers on this

topic). There is no reason to suspect that predatory behaviour would

be immune to the effects of early social experience, so rather than

dismiss the question it must be tackled head on and a number of inves-

tigators have attempted to do just this.

The late Zing-Yang Kuo's classic experiments with the domestic

cat represents the first major attempt (Kuo, 1930, 1938). In one
of his experiments Kuo socially isolated 20 cats at an early age and
tested their reaction, starting from the age of six days, to the
following types of prey: a wild rat, a domestic rat and a wild mouse.
Testing continued until a subject had killed all three types of prey
or until it was 120 days old. Kuo found that one of his cats killed
as early as 45 days and that eventually nine of the twenty (45%) killed
at least one type of prey before testing was terminated. Unfortunately,
this result of a 45% incidence of killing in isolated reared subjects
is somewhat difficult to interpret; that is, did it facilitate or
inhibit killing? This is so because Kuo failed to include a control
group (i.e. socially reared kittens) hence he had nothing to compare
the result against. What effect social experience rather than lack
of social experience might have had on the development of prey killing
is point Kuo overlooked but nevertheless this widely cited study is
significant in that it clearly demonstrated that social experience per
se was not necessary for the development of the prey killing response.

After a long absence from a research into animal behaviour, Kuo,
some 30 years later (see Kuo, 1960) again raised cats in social isola-
tion - this time not for four months but instead for ten months. In
addition, he raised dogs in isolation for the same length of time.
Further, this experiment contained the appropriate control groups;
i.e. dogs and cats who were raised with conspecifics. Testing commen-
ced at ten months of age and besides testing them with rats Kuo also
offered several other prey species such as birds, rabbits and guinea
pigs. His results showed, unequivocally, that early social isolation

greatly enhanced the predatory tendencies of both the cats and dogs when compared to their socially reared counterparts.

Domestic rats have also been the subjects in a number of social isolation experiments. For example, Myer (1969) examined the predatory behaviour of a group of rats that had been raised in isolation for four months. The control group consisted of rats who were reared in groups of four for a similar period of time. For testing purposes Myer found it necessary to split up the communally reared groups so that they could be tested individually; thus these communally reared rats were isolated and subsequently given ten days to adapt to their new living quarters before being exposed to the prey. Testing consisted of presenting a mouse once daily into a subject's own individual cage and continuing this procedure until the criterion of killing or failing to kill on ten successive tests was met. Myer found no significant difference between the two groups in terms of number who killed (62% of the communally reared subjects as opposed to 57% of the isolates), however, he observed qualitative differences in the killing response. Isolated rats were 'poorly co-ordinated' in their attacks whereas the killing response of the socially reared subjects was 'smooth, rapid and well-integrated'.

Again working with rats but offering frogs as prey, Johnson, DeSisto and Koenig (1970, 1972) found that rats raised in isolation killed significantly more often than littermate controls raised with peers. In this study 80% of the isolated rats killed compared to only 49% of the rats raised in groups.

This finding is in obvious conflict with the finding of Myer reported above. How can these differences be reconciled? Johnson and his colleagues suggest that the differences might be explained in terms of the testing procedures used in each of the experiments. For example, in their experiment rats were tested in a neutral area while in the experiment of Myer rats tested in their own individual home cage. By testing rats in a neutral area Johnson et al. obviated the necessity of having to break up the communally reared groups for testing purposes (i.e. the communally reared rats were tested individually in the netural area and then immediately returned to their group) thus they never experienced any isolation whatsoever. Myer, on the other hand, as indicated, isolated his subjects for a period immediately prior to testing and this brief period of isolation could, in part, account for the discrepant findings. Johnson et al. themselves explain, "the failure of Myer to obtain a difference between the isolated compared to the group reared rats may be due to procedural variables such as the use of mouse killing as a test of aggressiveness or the isolation of group reared rats for ten days before being individually tested with mice" (1972, p-238).

Thus it appears that a period of social isolation immediately preceding a test could have some influence on the rat's predatory response. Pion (1969) has come forth with some evidence which gives additional support to this belief. In his experiment Pion took proven adult non-mouse killing rats and housed them in social isolation for a period of 14 weeks. Pion found that this treatment had the effect of converting 50% of the non-killers into killers. The finding of

Bernstein and Moyer (1970) is likewise in accord with this for they also found that the incidence of mouse killing by rats could be increased through a period of social isolation immediately preceding a test.

From the studies reviewed in this section one may tentatively conclude that social isolation has the general effect of increasing the likelihood of the predatory response. As indicated, this has been found to occur in both rats and cats. This finding is not surprising considering the pervasive effects social isolation has on other types of behaviour. It is important, however, that more detailed studies be conducted on this topic. For instance, the relationship between isolation induced predation and isolation induced aggression of the other types (Moyer, 1968) still needs to be worked out. If predation is a form of aggression as Moyer claims then how does it vary with inter-male aggression, maternal aggression, etc. as the result of social deprivation ? That is, do the factors which affect the other kinds of aggression influence predation in the same way (i.e. rate of metabolism of brain amines, age at isolation, degree and type of isolation, species being isolated) ? Further, if differences were found between species then how do they relate to socio-ecological variables ?

Cross-Species Socialization

The reason why social isolation causes an increase in the cat's or rat's predatory response is not exactly known but it has been theor-

ized by some (for example, see Lagerspetz and Heino, 1970;   Scott,

1958, 1966, 1973 or Scott and Fredericson, 1951) that early social

contact enables animals to learn not to be aggressive. It is bel-

ieved that conspecifics early in life become socialised onto each

other and such socialization in turn serves to inhibit any aggressive

tendencies which might later arise within the individual. Because of

this a number of investigators have attempted to socialise a predator

onto its prey. Through such socialization it was thought that any

hostile tendencies a predator might have (towards prey) would be

inhibited.

Kuo addressed himself to this problem in several studies (see

Kuo, 1930, 1938, 1960). In the first he housed domestic cats with

a single prey species (either a domestic rat, a wild rat or a dancing

mouse) from the age of six days onwards. Prior to weaning the prey

remained in a kitten's living quarters for about twelve hours per

day (at which time the mother was removed; Kuo felt that if the

mother was present she herself might have killed the prey) and sub-

sequent to weaning the kittens lived in continuous social contact

solely with the prey - no other conspecific was present. Testing

commenced at six days of age; this consisted of removing the mother

and the familiar prey with which the kitten was living and presenting

to it, in succession, a domestic rat, a dancing mouse and a wild rat.

Immediately after each test the familiar prey companion was placed back

in the kitten's cage. Tests were conducted every four days and contin-

ued until a kitten had killed all three types of prey or until it was

120 days old. Kuo found that only three of his eighteen kittens killed

prey before they reached the age of 120 days and those which did kill

never killed the type of prey with which they had been living. Rather than kill most kittens exhibited a great deal of friendly or compassionate behaviour such as cuddling up to and fondling the prey. Often during a test a kitten directed 'protective' responses to the prey, similar in kind to the protective responses a mother cat shows to her young. Kuo further observed that the temporary removal of the familiar prey from the kitten's cage cuased it to become extremely restless, mew excessively and search from corner to corner in an attempt to locate its 'companion'. In short, Kuo felt that his kittens had become socialized onto the prey and this in turn served to inhibit any predatory tendencies they might have had towards it or to the other unfamiliar prey objects with which they were tested. Kuo characterises this unusually strong attachment by anthropomorphically saying: "protective responses and responses of attachment as described above are really what the traditional psychologists call manifestations of 'love'. Indeed, if cats have an instinct of love, certain of my kittens have shown it in their responses to rats" (1930; p-26).

In a follow-up study with cats Kuo (1938) again demonstrated that early socialization onto the prey species could prevent the development of the predatory response. In this study besides raising his cats with rats Kuo also raised them with sparrows and found that this procedure was partially effective in dampening a cat's response although it did not completely eliminate it. That is to say, some cats continued to kill the birds. Further, in this experiment, cats were not raised solely in the company of rats or birds but also with several members of their own species. This procedure had the effect

of redirecting the cat's affectional and compassionate behaviour from the prey to the conspecific. Thus, this finding is noteworthy in that it demonstrated that a cat will direct most of its social responses to its own kind when given the choice between a conspecific and a non-conspecific.

Again working with cats and, in additon, with dogs as well, Kuo (1960) in another experiment regularly exposed an experimental group to various prey objects (rats, birds, guinea pigs) during the first ten months of their lives. The results of this experiment confirmed his previous findings in that cats and dogs who received this early exposure tended to behave in a friendly or indifferent way when tested; control subjects who never experienced prior exposure usually behaved with hostility and aggression.

Other investigators have reported experiments in which rats were exposed to their potential prey for a protracted period early in life. For example, Myer (1969) raised rats communally with mice, commencing shortly after weaning and continuing until 150 days of age. Subjects in a control group never received this exposure. At 150 days rats in both groups were individually caged and after a ten day adaption period they were tested for mouse killing. The results confirmed the hypothesis that rats, like cats, could become socialised onto their prey through early exposure. In this experiment 54% of the subjects in the control group killed as opposed to only 9% of the experimental subjects. Myer also found that the effects of early exposure were fairly permanent for after the initial series of tests a re-test was conducted two months later (rats were never exposed to mice during the

test - re-test interval) and it was again found that the incidence

of killing in the control group remained significantly higher than

the incidence in the experimental group. Other investigators

(Denenberg, 1971; Denenberg, Paschke and Zarrow, 1968) have corrob-

orated this basic finding and in addition Galef (1970) found that the

predatory tendencies of wild rats could be inhibited through prolonged

early exposure to mice.

Pion (1969) logically followed up these experiments with one

of his own in which he exposed rats not to the mice themselves, but

only to their odours. When removed from the odours and tested Pion

found only 2% incidence of killing. He thus concluded: "the presence

of the mouse odor alone is effective in reducing killing" (p-10).

Additional research with the cross-fostering technique has

shown that the probability of socialising a rat onto its prey may

depend to a large extent on the type of prey species used. Take,

for example, the research reported by Johnson and associates (Johnson,

DeSisto and Koenig, 1970, 1972). In one of their experiments rats

were reared in the following conditions: 1) rats reared communally

on an elevated platform in the middle of a partially filled bathtub

which contained frogs; 2) rats reared communally in a cage that

contained a shallow pan of water in which a single frog was maintained;

3) rats reared communally in a cage that contained a single frog

enclosed in a transparent box (rats in this condition could see and

smell the frog but not touch it); 4) rats reared individually with

a frog enclosed in a glass jar; 5) rats reared communally in cages

which contained a glass jar holding giant cockroaches; and

6) rats reared communally without exposure to the cockroaches. This

experiment was cleverly designed for it not only examined the effects

of communal versus solitary rearing but also the effects of different

types of exposure to the prey. That is, Groups one and two had

complete social exposure in that they were allowed to physically

interact with the prey, while Group three had only visual and olfact-

ory exposure. Group four had even less - just visual exposure.

Likewise, the rats in Group five were allowed only visual exposure

to the cockroaches.[11]

On the whole the results of this experiment showed that rats

could not become socially attached to the prey species with which

they were raised. In fact, exposure to the frogs, whether it be

direct physical contact or just visual and olfactory contact,

served to enhance the tendency to kill when tested. Isolated rats

raised with protected frogs (Group four) killed more often than

those subjects raised in isolation without any exposure.[12] Likewise,

---

11. These experimenters did in fact try to raise rats and cock-
    roaches together without any physical barriers but the attempt
    had to be abandoned because the rats started to attack and eat
    the cockroaches. It should be remembered that the aim of this
    experiment was to expose rats to their potential prey in order
    to determine what effect it had on later prey-killing tendencies;
    thus the whole purpose of the experiment was defeated if a rat
    killed and ate the prey before the actual test.

12. This latter group was derived from an earlier experiment
    reported in the same paper. Johnson et al. use it here as a
    control group for comparative purposes.

rats raised in groups with exposure to frogs (Groups one, two and three) killed more often than those subjects raised communally but without exposure.[13] Exposing rats to cockroaches (Group five) seemed to suppress killing to some extent when compared to subjects in the control group (Group six); the incidence of cockroach killing in the experimental group (Group five) was 60% and in the control group it was 82%; however, this difference did not reach statistical significance.

· Thus cohabituation rearing between a rat and a frog, and a rat and a cockroach, failed to result in social attachment; consequently, there was no reduction in a rat's predatory tendencies. In fact, as indicated, when frogs were used as prey there was an increase in the likelihood of killing. Now this result is inconsistent with previous findings, that is, those of Kuo and Myer, and further it runs counter to the effects supposedly produced by early socialisation. Why, then, did Johnson et al. fail in their attempt ? Johnson et al. reckon that the reason why their rats failed to form an attachment was because they could not get emotionally aroused in the presence of a highly dissimilar prey. Emotional arousal, Johnson et al. believe, is dependent upon stimulus similarity and since rats are so physically dissimilar from both frogs and cockroaches no arousal could occur; hence no attachment. They clearly state their position by saying: "It may be argued that social attachments are facilitated by emotional arousal and that such arousal in turn is influenced by stimulus

---

13. Again this latter group was derived from an earlier experiment.

similarity. It is not that dissimilar species fail to attend to

each other, but rather they failed to get emotionally involved.

.......It may be hypothesized that highly dissimilar species tend

to ignore each other or else engage in predatory behaviour, and in

either case emotional arousal is minimal which reduces the likeli-

hood of attachment formation" (1972, pp 240 - 241).

The effects of social competition

Another experience believed necessary for the development of

predatory behaviour is that of social competition. Generally speak-

ing competitive behaviour may be regarded as any social behaviour

directly associated with the attainment of a desired goal object.

In many cases of social competition the behaviours involved are of

the aggressive type; hence many workers have come to regard aggression

associated with the attainment of an immediate need such as food,

territory or sex partner as competitive aggression; on the

other hand, aggressive behaviour not immediately concerned with such

needs has come to be regarded as non-competitive aggression. Using

this distinction several investigators have attempted to relate an

animal's proficiency in competitive and non-competitive situations

with the tendency to capture and kill prey. These studies will be

reviewed in this section.

On the speculative level, Leyhausen (1973) maintains that early

competitive experiences an animal receives with littermates are valuable

for they serve to generate 'excitement' within the individual.

According to Leyhausen such excitement enables an animal to overcome any inhibitions it might have about killing prey. Like Leyhausen, Ewer (1968a) expressed the belief that competition generates the excitement needed for the development of killing. In fact, Ewer claims that she once induced her pet meerkat which normally never killed, to kill, by pretending to capture and kill the prey herself. Supposedly by doing this Ewer placed her meerkat in a competitive situation which apparently was all that was needed in order to raise the animal's level of excitement high enough so that it could make the kill itself.

In accordance with these beliefs Karli (1956) postulated that one reason why feral rats exhibited a greater incidence of killing than domestic rats (it will be recalled that the incidence of killing in the feral and domestic types was 70% and 10% respectively) was because they came from an environment in which competition for such commodities as food and shelter regularly occurred. Naturally, Karli reasoned, domestic rats never had the opportunity to experience these kinds of competitive interactions in captivity.

Kuo (1960) was the first to put this social competition hypothesis to an experimental test. Working with cats and dogs he attempted to keep all competitive interactions between his subjects to a minimum. He did this by training his animals to eat peacefully from a communal feeding dish. His control group received no such training. Kuo felt that this procedure would eliminate any competitive tendencies (e.g. fighting over food) an animal might have had in the feeding

situation. Apparently, Kuo's training programme was effective for

he reported that he rarely observed fighting over food in the experi-

mental group, while on the other hand, animals in the control group

(i.e. those who received no such training) regularly fought.[14] In

addition to eliminating competitive fighting over food, Kuo further

attempted to eliminate the spontaneous type of playful fighting

(e.g. non-competitive aggression) between his subjects in the experi-

mental group. He accomplished this by the unorthodox means of

spraying water into the face of an animal whenever it began to fight.

No attempt was made to curb the playful fighting of the dogs and

cats in the control group. So in essence what Kuo had in this

experiment was a control group who had undergone competitive and

aggressive experiences early in life as opposed to an experimental

group which lacked these experiences. Treatment continued for the

experimental animals throughout the first ten months of their lives.

At ten months testing commenced and the results Kuo obtained confirmed

his hypothesis. Control animals when confronted with the prey reacted

with what Kuo calls hostile or attack behaviour while the behaviour

of the experimental subjects was characterised as being either

friendly or indifferent.

Competitive experience was also thought to be necessary for the

development of mouse killing by rats. As mentioned, Karli (1956)

thought this to be so, and Heimstra and Newton (1961) conducted an

---

14. For details of the procedures involved in this training programme
    (Kuo refers to it as the 'dining car etiquette') consult the
    original article (Kuo, 1960, pp. 213-216) for they are lengthy.
    Basically, it consisted of punishing an animal by temporarily
    removing it from the feeding dish whenever it began to fight.

experiment to test this hypothesis. In their experiment these

authors allowed matched pairs of albino rats to compete for a small

supply of food which was accessible to only one animal at a time.

Rats in the experimental group received this type of competitive

training for 15 days and at the start of each session each rat was

under 22 hours food deprivation. The control group consisted of

rats who were neither food deprived nor trained to compete for food.

During the competitive sessions the experimenters made note of the

amount of time each rat spent in control of the food hopper for this

provided a measure of dominance. At the conclusion of training rats

in both groups were tested for mouse killing and the results showed

the incidence of killing was 55% in the experimental group and 0%

in the control group. Further, Heimstra and Newton observed that

of the 22 rats in the experimental group which killed 16 were dominant

during training. These findings led these authors to conclude:

"Of the various forms of behaviour, such as general activity, social

behaviour, fighting and food competition, shown by the animals in

the test situation, either fighting or food competition would appear

to be the most logical factors that would contribute to the develop-

ment of the killing response" (p-100).

Unfortunately the design of Heimstra and Newton's experiment

was methodologically unsound, for their experimental group prior to

testing experienced both food deprivation and competitive training.

Thus Whalen and Fehr (1964) reasoned that it could just have been

food deprivation and not competitive training which produced the

observed effect. To test this hypothesis Whalen and Fehr went on to

conduct an experiment in which they assigned rats to the following

three groups: 1) rats put on a cyclic food deprivation schedule and

given no competitive training; 2) rats both food deprived and given

competitive training; and 3) rats neither food deprived nor given

competitive training.[15] At the completion of training rats in all

three groups were tested for mouse killing and it was found that the

rats who were just food deprived (Group 1) killed more often than the

rats in the other two groups. These findings thus confirmed Whalen

and Fehr's original expectations but in doing so they contravened

the findings of Heimstra and Newton.

Whalen and Fehr accounted for these differences by theorizing

in a highly speculative manner. For instance, they assert that their

rats could have learnt habits during competitive training which

interfered with the habits acquired during cyclic food deprivation.

According to this view the habit which resulted from food deprivation

was that of biting. These authors contend that an animal's biting

habits increased at the time of stimulus change (e.g. when the food

was dropped into the cage) and such habits generalized to the situa-

tion when the mouse was put into the cage; hence it led to killing.

These authors also maintain that rats who were food deprived and

given training showed a relatively low incidence of killing because:

1) these animals learned to discriminate between food and another

animal, hence their biting habits did not generalize during the

test, and 2) competitive non-biting habits interfered with the biting

habits learnt during the time of feeding.

---

15. Like the rats in Heimstra and Newton's study, the rats in this
    experiment were trained to compete for a small supply of food.

Heimstra (1965) questions the validity of these speculations by conducting another experiment of his own. Again using rats, he assigned subjects to the same three conditions Whalen and Fehr employed in their study. His results showed that rats which were both food deprived and given competitive training killed significantly more often than rats in the other two groups. Thus these results confirm Heimstra and Newton's earlier finding but once again oppose the findings of Whalen and Fehr. How then can these differences be reconciled? Heimstra, still holding firm to the belief that competitive experience plays a role in the development of mouse killing, reasons that the discrepancies could have possibly been due to the strain of the rats utilized in each of the experiments. In Whalen and Fehr's study rats of the Sprague-Dawley and Long-Evans strains were used, while Heimstra in his study exclusively used rats of the Wistar strain. Thus Heimstra reasonably argued that the experience of the competition may not have had the same effect on the rats of the different strains.

Some evidence that runs directly counter to the belief that competition fosters the development of killing in rats has been presented by Myer (1969). In an attempt to identify the factors associated with killing Myer made comparisons between killers and non-killers on several measures such as litter size, body weight at weaning and body weight at the time of testing. Myer found no significant difference between killers and non-killers on any of these attributes; hence he concluded, "the failure to find any relationship between killing and litter size or weaning weight suggests that competition for food before weaning is not an important

determinant of the behavior" (p-48).

Up to now we have been mainly concerned with the effects of competitive aggression which, as mentioned, is one type of social competition. As noted, the evidence is a bit controversial as to whether or not this kind of experience fosters the development of prey killing. We will now take a look at the effects of another type of social experience, namely that of non-competitive aggression. It should be remembered that non-competitive aggression is simply another name for fighting behaviour, or behaviour which has commonly been referred to as intra-specific aggression or agonistic behaviour. It differs from competitive aggression in that the animals fight 'spontaneously'; that is to say, there is no ostensible goal object present in the environment which might act as a catalyst for the behaviour. Competitive and non-competitive aggression are similar, however, in that they both involve fighting, and further both irrevocably lead to the formation of dominance hierarchies.

The results generated from the non-competitive studies, like the results from the competitive studies, are somewhat equivocal. Working with rats, both Johnson, Reich and DeSisto (reported in Johnson, 1972), and Baenninger and Baenninger (1970) reported that they could find no relationship between a rat's success in fighting and the tendency to kill mice. With mice however the story is different. As mentioned, Thomas (1969) tested two strains of domestic mice for cricket killing. Subsequent to testing she housed subjects from each strain communally, observed their spontaneous fighting, and found that the strain quickest and most efficient in cricket killing

were also the most aggressive and dominant fighters. Thus what emerged for Thomas was a positive relationship between predation and intra-specific aggression.

Several investigators have also tried to relate an animal's social status, or its position in a dominance hierarchy, with the tendency to kill prey. The results from these studies show un-equivocally a relationship between these.two variables. For example, Karli, Vergnes and Didiergeorges (1969) reported that if a mouse was introduced into the cage of two well-established killers it was usually the dominant one which did the killing. DeSisto and Huston (1970) also found that if a frog was introduced into a cage contain-ing several domestic rats it was usually only one, the most dominant, which killed. During the introductions the most submissive rat usually remained at the back of the cage well out of the way of the most dominant. Clark (1962a) working with grasshopper mice obtained the same result. The prey killing behaviour of several species of felid also seems to be affected by social status. For instance, Leyhausen remarks, "social ranking among other factors greatly influences the speed with which an individual develops into a per-fect killer" (1973, p-243).

If the reader has followed closely what has been said in the last several paragraphs he will have noticed that the findings of Johnson, Reich and DeSisto (reported in Johnson, 1972) and those of Baenninger and Baenninger (1970) apparently conflict with the findings of DeSisto and Huston (1970), and Karli et al. (1969). It will be

recalled that both Johnson et al. and Baenninger and Baenninger

could find no relationship between a rat's intra-specific aggression

and the tendency to kill prey. On the other hand, both Karli and

DeSisto and Huston, found a clear relationship between these two

variables. Now it would be reasonable to expect the most aggressive

rats to be the most dominant, and likewise, the most dominant, the

most aggressive.[16] If this was so then one would therefore expect

to find a relationship between aggression and prey killing; however,

as mentioned, this was not what Johnson et al. or Baenninger and

Baenninger found. More than likely this discrepancy can be traced

to the method of testing used in each of the experiments. For

example, Baenninger and Baenninger tested their rats individually

while in the experiments of Karli et al., and DeSisto and Huston, rats

were tested in groups.[17] It can therefore be argued that intra-

specific aggression in itself is not related to prey killing, but

when tested in groups the most aggressive are the most dominant and

therefore are at an advantage for their aggression allows them to

gain access to the most favourable object in their environment (in

this case the mouse); hence they are the ones who usually do the

killing.

---

16. This assumes that dominance is a uni-dimensional trait; that
is, intra-specific aggression correlates with other standard
measures of dominance, such as preference in feeding, access
to females, nesting in favourable sites, etc.

17. Johnson, Reich and DeSisto's article has not yet been published
so details of the testing procedure are not known; however, it
is likely that they also tested their subjects individually.

The effects of observational learning

Another experience an animal undergoes which has been found to have some effect on the development of prey killing is that of witnessing a kill. A number of investigators have reported that animals who initially would not kill would begin to do so after observing the killing behaviour of a conspecific. Kuo (1930) found this to be the case with domestic cats. In his experiment Kuo took proven non-killers and exposed them regularly, from approximately 120 days to six months of age, to a 'rat killing' environment.[18] This rat killing environment consisted simply of placing a rat directly in front of a non-killers cage so that it could then be killed by a highly efficient killer. Apparently this treatment was quite effective for it successfully converted nine of Kuo's eleven non-killers into killers.

Of some interest, however, was Kuo's failure to induce killing, through this same procedure, in non-killer cats that had been previously raised with rats. It will be recalled that in one of his experiments Kuo reared cats with rats through the first four months of their lives and found that very few cats would kill if reared in this way. Thus Kuo reasoned that possibly these non-killers could likewise be induced to kill if they too were exposed to the rat killing environment. Kuo did just this, however, surprisingly, it was found that this treatment had virtually no effect on their pred-

---

18. These non-killers had been previously raised in social isolation and tested for rat killing between the ages of six and 120 days. The experiment from which these animals were derived has already been described (see Section 2.4b.4a: The effects of social isolation).

atory tendencies. Only one of the 15 rat reared cats killed; thus

he concluded, "this clearly indicates that it is extremely difficult

to make a cat kill a rat if it has grown up with rats in the same

cage since it was very young" (1930, p-14).

In addition to exposing non-killers to a rat killing environ-

ment Kuo (1930) conducted another experiment in which he regularly

exposed a group of naive cats, from birth to 120 days, to this type

of environment. This treatment proved to be extremely effective for

it was found that 85% of these subjects killed when tested. Kuo

compares this result to the 45% incidence of prey killing in cats

who were raised in social isolation and never allowed to witness the

killing behaviour of a conspecific.

The findings from the laboratory with the domestic cat are in

general accord with what has been observed in the field by etholog-

ists. For example, Eaton (1970), who studied the ontogeny of prey

killing in the cheetah, discovered that young cheetah cubs may depend,

to an extent, on observational learning for the development of their

prey killing techniques. Eaton found that it was the mother who

provided the model from which the cubs could copy. Initially, he

noticed, that the young cubs would simply follow and remain close

by the mother whenever she killed prey. Never did they take part

in the killing themselves; supposedly they only observed. Event-

ually the mother would bring partially killed prey back so that the

cubs could kill it themselves with her assistance. When this happened

it appeared to Eaton that the mother was giving her cubs 'lessons in

hunting'; thus he concluded, "the adult cheetah is probably a

requisite for the cubs to learn to catch and kill prey" (p-502).

It appears that the domestic rat also benefits from a period

of observational learning. Pion (1969) reported an experiment in

which he allowed naive rats to witness mouse killing from the age

of three weeks to three months of age. When tested at three months

over 70% of the rats killed. Pion compares this result to the rela-

tively low incidence of killing (30%) in rats who never experienced

this treatment.

In another study with rats, Johnson, DeSisto and Huston (1972)

again demonstrated the positive effects of observational learning.

In their experiment these authors let proven non-killers witness

the frog killing behaviour of conspecifics. The control group

consisted of non-killers who were never permitted this experience.

When tested 57% of the experimental group killed; this compares

with a 25% incidence in the control group.

The studies reviewed so far in this section represent virtually

all that has been done concerning the effects of experience prior to

the test situation. To recapitulate, the major areas of concentra-

tion have been concerned with such variables as social isolation,

early exposure to the prey, social competition and observational

learning. Additional investigations which do not fall into any of

these categories have been reported by Galef (1970), Paul (1972) and

Pion (1969). Pion found that the incidence of mouse killing by domes-

tic rats was directly related to the size of the enclosure they were reared in; pups reared in spacious pens killed more often than caged reared controls. Galef working with wild rats found that handling them in infancy or rearing them with domestic rat mothers had no significant effect on their mouse killing tendencies. Lastly, Paul (1972) found that rats fed dead mice prior to their initial test for mouse killing would kill more often and with shorter latencies than rats fed just laboratory chow.

In summary, the evidence suggests that the experience an animal undergoes preceding the actual test - the test situation being defined as the time when the predator is actually given the opportunity to capture and kill - could have a profound influence on its prey killing behaviour in the test situation itself. As noted, some prior experiences serve to reduce the likelihood of killing (social rearing with the prey species) while other experiences act to increase the chances considerably (witnessing a kill and social competition). Further, some of these experiences occur early in an animal's ontogeny (social rearing with the prey species and social isolation) while others occur relatively late (witnessing a kill and social competition). With this background we will now proceed to examine what effect experience within the test situation has on the development of the predatory response.

2.4b.4b. The Effects of Experience Within the Test Situation

The effects of practice

It seems as though most predators need the experience of interacting with the prey before they can become sufficiently motivated or skilled to kill in a rapid and efficient manner. This basic finding has been stressed by both psychologists and ethologists alike (see Kuo, 1930, 1960 and Leyhausen, 1956, 1973, for felids; Ewer, 1968b, 1969 for marsupials; Fox, 1969, 1971 for canids; DeSisto and Huston, 1970 and Myer, 1968, 1971 for the domestic rat; Thomas, 1969 for domestic mice). If this be the case, how then does a predator behave when it is first given the opportunity to interact with the prey, and in what ways does its behaviour change after its acquired some experience?

Take the domestic cat for example. Ewer (1968a) writes:

"When the kitten is $2\frac{1}{2}$ - 3 months old, it normally encounters its first live prey, brought in for it by its mother. As soon as the prey runs the kitten will chase after it and may then make a kill with a prefectly oriented neck bite. Often, however, there is hesitancy and it may be some time before the kill is made. At first the factors responsible for the variation in performance remained mysterious. By filming and analysing exactly what happened, Leyhausen was finally able to show that before the oriented bite to the constriction at the back of the prey's head can be released, a certain level of excitement must be reached. This is required to overcome the inhibitory influences exerted by the unfamiliar and possibly dangerous prey. This excitation may be built up by prolonged 'play' with the prey" (p-320).

From the above passage it can be seen that when a naive cat encounters its first live prey it may behave in one of two ways;

namely, either with a perfectly oriented neck bite, or alternatively, with a prolonged period of play. It is essential that both of these possibilities be considered for most of the theories dealing with the development of the cat's predatory behaviour take into account each of these possible alternatives.

Consider first the cat's playful behaviour.[19] What functions does such play with the prey serve? According to Leyhausen (1973) and from what Ewer has said above, play serves to build up 'excitement' within the individual. Supposedly, without such excitement a cat's level of arousal in the presence of the biologically appropriate releaser (the prey) remains low (due to the inhibiting factors of novel and potentially dangerous prey) and therefore it is unable to deliver a bite of sufficient strength for killing to occur. Further, Leyhausen maintains that this necessary excitement is often derived earlier in ontogeny through competitive interactions with littermates.

A more traditional view holds that through a period of play with

---

19. Fox (1969, 1971) has also observed play prior to a kill in several canid species (wolves, foxes, coyotes, dogs). Playful behaviour consisted of pawing and stabing with the forepaws, picking the prey up in the mouth, throwing and then retrieving it and even on occasion presenting the play soliciting posture. In addition to the accounts of play with the prey in Carnivora, Blossom (1932) observed the shrew, playing with an insect prior to a kill. Other than these reports no one to this author's knowledge has reported playful behaviour of this sort in any other animal order. Ewer (1963, 1969) emphasised the fact that her meerkats and marsupials never played with the prey prior to a kill and likewise no one has ever reported playful behaviour in the more commonly studied rodent species such as rats and grasshopper mice.

prey felids learn to perfect, organize and practice their prey kil-

ling techniques. For instance, Schenkel (1966) regards the period of

play as 'hunting exercies' in which the predator (lions in this case)

learns the proper prey killing technique. Ewer (1968a) is also in

accord with the belief that a period of play provides a sort of train-

ing period in which a great deal of learning takes place. She writes:

> "Play results in discoveries. This can be seen very
> clearly in a kitten's play with a ping-pong ball. A
> cautious approach to the unfamiliar object is followed
> by the usual tentative pat with the paw. The ball moves
> and provides the ideal releaser of chasing behaviour:
> 'small object moving away'. Very soon the kitten is
> involved in a new game in which it dribbles the ball with
> increasing speed and skill, using alternative movements
> of the forepaws to keep it in motion. The kitten is using
> here exactly the same movements as it does when pursuing
> a mouse.... What the playing kitten has done is to learn
> how to use these movements out of its innate repertoire
> to control the ping-pong ball. In short, in play, the
> animal is experimenting with the relationships between
> its own actions and the external world and is learning
> all the time as a result" (p-298).

What is obviously implied in the above passage is that the cat

through its experience in the play situation learns in the words of

Ewer "how to use these movements out of its innate repertoire". If

this is so then let us digress somewhat and ask just what sort of be-

haviours does the cat possess in its innate repertoire?

In the example Ewer implicitly refers to the cat's paw movements

and elsewhere (Ewer, 1969) she has stated: "in the cat the most imp-

ortant thing that is learnt is how to use the innate repertoire of

paw movements so as to produce the correct situation for the killing

bite" (pp. 35-36). Moreover, besides coming into the test situation

with an innate set of paw movements Leyhausen has further postulated that a cat comes equipped with an innate disposition to bite wherever there is a constriction on the prey which normally is where the head joins the body, in other words the neck. Leyhausen (reported in Ewer, 1968a) conducted an experiment to test this supposition by presenting cats prey dummies that were either normal, headless, or with the head removed and stitched onto the posterior end. His results showed that the cats tended to bite wherever there was a constriction, thus lending support to his theory.

Ethologists also maintain that other species come into the test situation with a basic set of innate responses. Wustehube (1960) who studied prey killing in the polecat concluded, "the complete prey-catching pattern with the killing bite in the nape of the neck is inborn" (p-612). Rasa (1973) who compared snake killing in experienced and naive mongooses also concluded, "the fact that naive animals responded ..... in essentially the same way as the experienced ones suggests that the main behavioural patterns involved in snake killing are innate" (p-461). In another part of her paper Rasa writes, "these observations suggest that the more specialized prey capture method 'high spring' must be considered innate since it appeared in the behavioural repertoire (of naive animals)[20] in a perfectly developed form" (p-477). In a similar fashion, Eisenberg and Leyhausen (1972) write, "Our observations would tend to support the theory that the naive carnivore (when first attempting a killing bite) will aim

---

20. Author's insertion.

for the head or neck if the prey is not too intimidating. Certainly

some learning is involved in adjusting the innate patterns to differ-

ent types and sizes of prey objects" (p-82). Further, predators possess

what ethologists long ago termed innate releasing mechanisms (IRM).

According to Eisenberg and Leyhausen, "It has been generally noted

that among the various stimulus elements acting on a given IRM those

consisting of movement usually have a far stronger effect than those

consisting of anatomical or colour patterns" (1972, p-81).

. This digression into the innateness of predation has taken us

away from the main issue at hand; namely the effects of practice.

However, it should be fairly clear that according to ethological

theory predators do in fact possess what ethologists call 'innate'

behaviour. In their writings ethologists seem to imply that the

innate responses are genetically pre-programmed to interact with

that which is acquired through learning and experience. More spec-

ifically, it seems as though the innate responses form the core or

structural basis onto which learning and experience are built. The

disposition to bite at the neck, the paw movements, the immediate

responsiveness to chase after small moving objects are all suggestive

of some ·inherent tendency to within the individual. Initially these

tendencies or behaviours are all that a predator needs in order to

kill; however, with experience it comes to learn how to use them

most effectively. Ewer (1968a) clearly expresses this point in the

following passage:

> "Once it has been released for the first time, killing
> becomes progressively more easily elicited and after the
> first few kills have been made the stage is set for learn-

ing to start taking a hand in the process of shaping
the responses.....The young cat's confidence increases
after it has made a number of kills 'correctly', almost
always refusing to attack except in the optimal situa-
tion, with the prey running away so that the strike can
be made obliquely downwards from behind. It now starts
to attack in more difficult situations. Because of this
its performance may seem to have deteriorated and the
killing bites may now be imperfectly oriented. The cat
is in fact learning how to utilise the (innate) move-
ments in its repertoire to deal with prey not in the
orthodox position.......the learning of this type of
skill does not affect the innate responses; their neural
basis remains unchanged and they still may be released
by the appropriate situation. (pp. 321 - 322).

Returning to our discussion on cat predation it may be said,

in summary, that according to ethological theory a naive cat has

the potential to kill when it first meets up with the prey. How-

ever, as stated, it usually does not because it lacks what Leyhausen

calls a state of excitement. Those exceptional cats which kill with

a neck bite on the first encounter are able to do so probably because

they derived the necessary excitement beforehand through competitive

play with their littermates. For most cats, though, the necessary

motivation is derived through play with the prey. Through such play

a cat will become highly aroused and this arousal in turn will trigger

the innate killing bite. In addition, it should be remembered, prior

play also serves a second highly important function; namely, it

enables a cat to practise the behaviour associated with capture and

killing. When it plays a cat learns to amalgamate its innate chunks

of behaviour, such as the neck bite and paw movements, into a func-

tional whole so that when it finally becomes sufficiently aroused it

will be able to kill in a rapid, efficient and skillful manner.[21, 22]

The fact that learning plays such a large part in the development

of mammalian predatory behaviour has led some authors to conclude that

a predator becomes more efficient or more skilled in killing after exper-

iencing several successful kills. (DeSisto and Huston, 1970; Ewer, 1969;

Thomas, 1969). In what sort of behaviours is such efficiency reflected?

For example, take the behaviour concerned with biting. Kreiskott (1969)

observed that naive rats tended to initially bite into different sections

of the prey and only after several successful kills did they come to

bite into the nape of the prey's neck. Likewise, DeSisto and Huston

---

21. Ewer (1968a) maintains that a cat's killing motivation can only dev-
elop during a certain 'critical period'. This critical period oc-
curs at the time in ontogeny when the cat is most likely to show
playful behaviour; in other words, fairly early. Leyhausen has also
incorporated this notion of a critical period into his theory. For
example he writes, "An innate behaviour pattern may not be shown or
develop much later if it is not released during a definite stage of
development by being brought above threshold level through additional
unspecific exciting influence" (Leyhausen, 1965 quoted in Rasa, 1973,
pp. 476-477).

22. In addition to play with the prey there is also the belief that play
with one's own conspecifics, aside from building up an animal's
level of excitement, also serves as sort of a practice period. This
is because that some of the behaviours that are directed towards
conspecifics in playful encounters, such as the neck bite and manip-
ulation with the paws, are likewise used to capture and kill prey
(Poole, 1966). To test this notion experimentally one would have
to deprive an animal of the opportunity to engage in play, and this
has been done by several investigators who raised their animals in
social isolation soon after weaning. It should be recalled that
Myer (1969) did this with domestic rats and found that his isolated
reared subjects were 'poorly co-ordinated' in their attacks when
compared to the socially reared controls who killed in a 'smooth,
rapid and well integrated' fashion. Eibl-Eibesfeldt (1961, 1963)
also reared polecats in social isolation and found that it took
these animals longer to learn the proper neck bite orientation when
compared to socially reared polecats. Similar results have been
obtained by Rasa (1973) for mongooses.

(1970) noted that inexperienced frog killing rats made their

initial attacks on the legs of the frog whereas experienced killers

usually made attacks directed towards the nape of the neck.[23]

Boice and Schmeck (1968) who studied the predatory behaviour of the

grasshopper mouse reported, "ontogenetic research indicated gradual

development of predation on insects, with learning improving the

effectiveness of the kill; i.e. biting into the head region rather

than elsewhere" (p-79). Eibl-Eibesfeldt (1961, 1963)in his studies

with polecats made similar observations. For example, he reported

that inexperienced polecats tended to bite into any part of the prey's

body and only after several encounters with the prey did they come to

learn to bite into the nape of the neck.[24] Ewer (1969) has also

observed that in several marsupial species the initial killing bites

were often poorly oriented, but with experience the animals learned

to aim their bites to the neck region of the prey. Further, Leyhausen

(1973) asserts that the killing bite of the domestic cat 'clicks into

place' after only one or very few successful attempts. According to

Leyhausen the cat "quickly grasps the advantage of biting into the

nape rather than other parts of the neck, and soon it has learned to

aim its bite purposely and exclusively at the nape" (p-244).

---

23. Because a rat's killing behaviour improves with experience does
    not necessarily mean that it too is founded upon innate behavioural
    elements. Most researchers who have worked with rats simply state
    that this species predatory behaviour improves with experience
    without ever making reference to any sort of innate behaviour.

24. This conclusion by Eibl-Eibesfeldt conflicts with Wustehube's
    finding which was reported earlier in this section. As it will
    be recalled Wustehube concluded, "the killing bite into the nape
    of the neck is inborn". Eibl-Eibesfeldt relates these differences
    to the fact that his polecats were raised in isolation while
    Wustehube's were raised socially. Since young polecats do grip
    each other by the neck in playful fighting Eibl concluded that
    they were in this way able to learn the correct orientation.

A predator's efficiency cannot only be measured in terms of where the killing bite occurs but also in terms of latency to kill and the frequency of other types of behaviour associated with killing. For example, DeSisto and Huston (1970), Karli (1956), Moyer (1971), Myer (1964, 1971) and Thomas (1969, 1972) all report a decrease in latency to kill with repeated testing. Myer noted that when a naive rat first encountered a mouse its latency to kill was relatively high. Rather than kill it behaved ambivalently (e.g. approach and withdrawal), explored, groomed or manipulated the prey with the forepaws. Often it would carry a mouse to the corner of its cage. On subsequent encounters, however, behaviours like these diminished; instead a rat came to attack and kill in a swift manner immediately after the prey was introduced. In the study of DeSisto and Huston (1970) these authors measured, in addition to latency to kill, the frequency and duration of prey exploration and nips at the prey. They found that both the frequency and duration of each of these behaviours decreased significantly with repeated testing. Thus it appeared to these authors that the more efficient a predator became the less time it spent exploring the prey prior to a kill and the fewer nips it needed in order to kill.

Myer's study (Myer, 1971) is particularly noteworthy because it demonstrated, quite clearly, that through experience in the test situation a rat's killing response can become highly consistent and stable. In his study Myer tested his rats at various ages (50, 100, 150 and 200 days of age) by offering mice once a day until they met the criterion of killing or failing to kill on ten successive days.

In addition, all rats were re-tested at 225 days of age; thus a
fairly lengthy period of non-exposure to the mice ensued between
the original test and the re-test (175 days for the rats who were
initially tested at 50 days). Basically, what Myer found was that:
1) Rats which killed at least three mice continued to kill in a
rapid fashion whenever tested. Very few reversals of the reaction
occurred; thus the killing response remained consistent. 2) All
rats which killed on the initial series of tests killed when re-
tested at 225 days; thus the killing response remained stable.
3) Some rats that failed to kill when initially tested killed when
re-tested. Further, the proportion of non-killers which later killed
was greater the longer the interval between tests; that is, most of
the non-killers which reversed their reaction came from the group
that was initially tested at 50 days of age.

How then does Myer account for these results? He argued that
the act of killing in its own right was a self-reinforcing event;
thus the tendency for a rat to engage in this behaviour was strength-
ened whenever it occurred.[25] Obviously this explains why the killing
latencies decreased with repeated testing and it further accounts
for the observed consistency and stability of the behaviour. Of more
interest, however, were the killing reversals that occurred in some
of the rats when they were re-tested at 225 days of age. Myer believes
that the reversals were brought about through the process of habit-
uation. He notes that those rats which did not kill on the initial

25. It is important to realize that Myer removed the prey immediately
    after a kill, thus the rats had no opportunity to feed on the
    prey. Hence killing was in no way reinforced through eating.

series of tests eventually stopped responding to the mice altogether
and what this obviously suggested to him was that these non-killers
habituated to their presence. Subsequently, however, during the test-
re-test interval the effects of habituation dissipated; thus on the
re-test the mouse was again relatively novel stimulus and this in
turn induced killing.[26] Further, the results suggested that the
amount of dissipation that occurred depended on the interval between
the initial test and the re-test; this then explains why most of the
rats who reversed their reaction came from the group which was init-
ially tested at 50 days of age.

Although Myer's use of the concepts of self-reinforcement and
habituation are quite reasonable explanations for the observed con-
sistency and stability of the response, he seemed to avoid coming to
grips with the important issue of why some of the non-killers, who
killed on the re-test, did not initially kill when exposed to the
mice; that is, before their reactivity had habituated. The nearest
Myer comes to answering this crucial question lies in his remark,
"the probability that a rat will attack and kill the first mouse that
it encounters is jointly determined by the strength of the rat's
tendency to attack and the extent to which the mouse provides attack-
inducing stimuli" (p-267).

Nonetheless, what Myer's study shows along with the previously
mentioned studies is that a predator will become more efficient and

---

26. Although this is the implied interpretation of Myer's explana-
tion, he nowhere explicitly states that novelty per se induced
attack and killing.

skilled in killing after a period of interaction with the prey. In

general, it has been found that those predators (both cats and rats

alike) who eventually kill, will initially groom, explore, manipulate

or even play with the prey. However, in subsequent encounters, after

the predator has acquired some experience through its interactions

with the prey, killing will occur and after several successful kills

the killing response becomes consistent, stable and stereotyped.[27]

Whether or not this experience acts on any innate behaviours or innate

dispositions probably depends on the species being studied as well as on

the bias of the investigator; that is, whether he be a psychologist or

ethologist. On the whole, it has been mainly ethologists who have

claimed that certain predators, like the domestic cat, possess innate

behaviours. According to the ethologist experience enables a predator

---

27. Obviously in this discussion we are more concerned with the
effects of experience on the behaviour of those subjects who,
in Myer's words, possess a strong attack tendency. Those sub-
jects who fail to kill after several successive prey presenta-
tions probably possess a weak attack tendency; hence experience
for them acts in an entirely different manner. For non-killers
experience probably serves to habituate any reactivity they might
have had towards the prey; therefore they eventually come to
behave with indifference or avoidance during subsequent prey
confrontations. Further, it is believed that non-killing
experiences act to strengthen what Miley and Baenninger (1972)
refer to as an inhibitory mechanism. According to these
authors, "killing of mice is viewed as a rat's normal response
to mice which may be interfered with by an inhibitory mechanism
which is strengthened by each successive occasion on which it
is employed" (p-388). Consequently a non-killing experience
has reinforcing properties for it acts to strengthen those
non-killing behaviours mediated by this inhibitory mechanism.
The fact that non-killers possess an inhibitory mechanism which
prevents them from killing has been stressed by Myer in his
theoretical discussions of the mouse killing phenomenon (see
Myer, 1964, 1971) and recently Spector and Hull (1972) and Miley
and Baenninger (1972) have attempted to link this mechanism
with several well defined neurophysiological substrates.

to learn how to use its innate equipment. Psychologists, on the

other hand, also strongly believe that experience within the test

situation (and for that matter prior to the test situation) plays

a paramount role in the development of the predatory response.

However, unlike ethologists, they have rarely maintained the exist-

ence of any sort of innate behaviour. The reason for this position

has already been explained (see discussion preceding Section 2.4b.4a).

The effects of electric shock

The experience of being shocked during prey encounter is another

kind of experience within the test situation that has been found to

exert a strong influence on the predatory response. Myer (1966, 1967,

1968) and his student Baenninger (1967, 1970; also see Myer and Baen-

ninger, 1966) have repeatedly demonstrated that mouse killing by rats

could be effectively suppressed through punishment with electric

shock. Such punishment, however, was found to be effective only if

it was administered just at the time when the rat started to attack.

Attack and killing were not suppressed by shocks uncorrelated with

or temporarily removed from attack. Once suppressed the effects of

punishment were found to be only temporary and not permanent; that

is, attack behaviour recovered during a test period subsequent to

suppression in which a rat never received shock if it attacked. More-

over, Myer (1967) found that the suppressing effects of shock depended

to a large degree on the rat's prior killing experience. For example,

those subjects who had been given extensive experience in killing prior

to the onset of punishment continued to kill longer (in terms of number

of trials to suppression) after the initiation of punishment and resumed killing sooner after punishment was discontinued (recovery period) than did rats who were inexperienced killers. It was further discovered that the time lag between the last suppression test and the start of the unpunished recovery tests had a minimal effect on the rate of recovery. That is to say, rats who had experienced intervals of one and four days between the two sessions recovered just as fast as those rats with intervals of seven days. This result led Myer to conclude that the recovery of the originally suppressed attack behaviour was primarily due to the extinction of the arousal of fear (such extinction was made possible by repeatedly presenting the mouse without the associated shock) and not simply due to the dissipation of the effects of shock which might have occurred as a function of time. Myer (1967) also found that both weak and strong shock were equally effective in suppressing the behaviour and Baenninger (1967) in another study paired a neutral stimulus (a buzzard) with shock presentation during suppression acquisition and found that the buzzard itself eventually came to act as a conditioned inhibitory stimulus.

One of the more interesting findings that has come out of this area of research has been that shock administered to suppressed killers (i.e. those subjects whose mouse killing behaviour had already been suppressed through shock) in the presence of mice can overcome the suppression produced by shock and consequently induce killing (Baenninger and Ulm, 1969; Myer and Baenninger, 1966). Thus shock has been found to have paradoxical effects. That is to say, in some cases it has been found to suppress mouse killing and in other cases

facilitate it. Myer and Baenninger (1966) account for these paradoxical effects in terms of two mechanisms which function to control a rat's attack and killing behaviour. First, they assert that an 'arousal' mechanism is present. This arousal mechanism acts to increase a rat's 'motivation' to attack. Once a rat has become sufficiently motivated for attack to occur then an attack threshold is transgressed and this in turn serves to trigger an 'attack' mechanism. This attack mechanism supposedly controls the behaviour after a sufficiently high level of motivation has been reached.[28] According to this theory, then, if a rat is punished for its attack behaviour a state of fear arises and eventually this fear becomes conditioned to the stimuli associated with killing. Thus when a rat is shocked several times for its attack behaviour the arousal of fear becomes intense enough to interfere with the arousal needed for killing. Consequently the attack mechanism is never activated; hence attack and killing never occur. Moreover, the suppressed killer can be subsequently induced to kill through shock mainly because such shock sensitizes the attack mechanism and such sensitization has the effect of lowering the attack threshold and, therefore, minimal arousal is needed for attack to occur. However, these authors further note that in order for attack and killing to occur under these circumstances then the suppressed killer must be confronted with the proper stimulus. For example, they note that suppressed killers will not attack rat pups when shocked, however, if shocked in the presence of a mouse attack and killing will readily occur.

---

28. This view is quite similar to Leyhausen's theory. It should be recalled that Leyhausen believed that a cat had to become sufficiently aroused, or excited, before it could deliver the killing bite.

Another important finding which emerged from the study of
Myer and Baenninger as well as from an earlier one by Karli (1956)
was that rats who never killed initially could not be made to do so
through shock. Myer and Baenninger reasoned that the failure to
convert these non-killers into killers through shock was probably
because of the simultaneous arousal of some other motivational state
such as fear, or possibly because these subjects had unusually high
attack thresholds to begin with, hence sensitization of their attack
mechanism could not occur.

Several investigators have also studied the effects of shock
on a cat's rat killing behaviour and in general the results have
shown that shock can likewise act in a paradoxical manner. For
example, Ulrich, Wolff and Azrin (1964) reported that a cat's killing
behaviour could be facilitated through shock; contrary to this,
however, Kuo (1930) reported that he successfully trained his cats
to fear a rat through similar shock treatment.

Whether or not shock facilitates or inhibits a cat's predatory
response probably depends on exactly when the shock is administered
and also on the size of the test enclosure in which the encounter
takes place. Concerning the former it is probably that shock admin-
istered to the cat just at the time when it starts to attack (i.e.
contingent shocks) will have the effect of making future occurrences
of attack and killing less likely. On the other hand, if shock is
administered to the cat prior to attack (i.e. non-contingent shocks)
then it is possible that this could help facilitate the behaviour.

In regards to the size of the test enclosure it could be argued that when a cat is shocked in a small enclosure it has no recourse other than to attack the object which apparently was responsible (at least to the cat) for the delivery of the shock, i.e. the rat. However, when tested in a large enclosure and shocked the cat alternatively has the opportunity to escape and will do so rather than attack. Both of these speculations are plausible, however, if they are to be substantiated more research is needed for apparently the studies of Ulrich et al. and Kuo are the only investigations to date which have been concerned with the effects of shock on rat killing by cats.

Lastly, it should be noted that Clark (1962a) reported that grasshopper mice would attack and kill domestic mice when shocked in their presence. In addition, Clark found that an originally neutral buzzard could come to control attack and killing if it was initially paired with shock.

The effects of environmental familiarity

In addition to shock another variable operating within the test situation which has been found to have a considerable effect on prey killing is that of environmental familiarity. In most laboratory studies researchers have made an effort to control for this factor; predators have usually been tested in their own familiar living quarters or in a test cage to which they were allowed to acclimatize. The reasons for these precautions are clear; several

investigators have found that a predator who was initially a
highly reliable and constant killer in its own cage tended not to
kill or kill with a great increase in latency after it had been put
into a novel environment (Avis and Treadway, 1971; Baenninger and
Ulm, 1969; DeSisto and Huston, 1970; Karli, 1956; Miley and
Baenninger, 1972).

Thus it seems, at least in the case of the rat, that a pred-
ator has to have a sense of familiarity with the environment in
which it is in before it will kill in that environment. Several
experiments by Karli (1956) best exemplify this point. In one
experiment he housed wild rats individually and then tested their
reaction to mice immediately after they were rehoused into new
living quarters or after an interval of two, five or seven weeks.
Karli found a low incidence of killing in those rats who were tested
immediately after being rehoused, however, the percentage of killers
increased with the time spent in the housing enclosure. Thirty per
cent did so after two weeks; 60% after five weeks and 70% after
seven weeks. In another experiment Karli took proven killers out
of their own home cages and tested their reaction to mice in a novel
circular pen. Again, he found that killing latencies greatly
increased when tested under these conditions; in some cases several
hours elapsed before killing occurred, but when the rats were placed
back into their own familiar home cages killing occurred in all
instances with very little delay. The results of these experiments
led Karli to conclude, "a wild rat kills mice more readily and with
shorter delays as it gets progressively adapted to the environment."
(p-95).

In another series of experiments DeSisto and Huston (1970) studied the effects of a novel environment on frog killing in domestic rats. Like Karli they found that by transferring an experienced frog killer from its own familiar home cage to a novel environment its killing latency could be greatly increased. DeSisto and Huston note that most rats when given a ten minute test did not kill at all; instead, the behaviour of most was concerned with exploring the surroundings into which they had been placed.

· The above mentioned investigations undoubtedly show that familiarity with the environment is a prerequisite if killing is to occur. Prior to this investigations were reviewed which demonstrated the profound effects electric shock has on the predatory response and preceding this literature pertaining to the effects of practice was reviewed. These three areas represent most of the work that has been done concerning the effects of experience within the test situation. In short, a predator needs the experience of being on familiar ground before it will kill. It further needs the experience of being able to physically interact with the prey in order to strengthen the tendency to kill and to perfect the prey killing techniques; and lastly, the experience of being shocked may either facilitate or inhibit the predatory response.

Other areas of investigation will now be discussed. First we will look at the effect hormones have on predation. Following this areas concerned with motivation and stimulus control will be examined. Again it will be apparent that most of the findings come from research

conducted with the white rat. Further, some of the research to be reviewed could well have been considered under the broad headings that have been dealt with already in the section on development; namely the effects of experience within the test situation and prior to the test situation. However, the three sub-topics chosen (the effect of hormones, motivation and stimulus control) are sufficiently broad enough and important enough to warrant coverage on their own.

2.4b.5. Hormones and Predation

Research on the endocrine basis of predation is scanty but the evidence which does exist points to the general and tentative conclusion that hormones exert relatively little influence. Take, for example, the direct effects of the male hormone testosterone. Karli (1958) reported that castration in adulthood had no effect on the killing behaviour of well-established male mouse killers. Further, he found that the administration of large doses of testosterone to established non-killers could not induce them to kill. These results are not surprising in view of the fact that most investigators have found no sex difference in the laboratory rat's tendency to kill (Bandler and Moyer, 1970; Karli, 1956; Lonoski, Levitt and Larson, 1973; however see Paul, Miley and Baenninger, 1971 for a strain - sex interaction) and, in addition, the fact that some rats will kill before they reach sexual maturity adds weight to the belief that testosterone plays a negligible role in the control and maintenance of the behaviour.

On the other hand, castration performed at an early age may

have some effect. Baenninger and Miley (1971) reported an experi-

ment in which they castrated male Long-Evans hooded rats on the

first day of life. Subsequently, these animals and unoperated

controls were housed communally until 90 days of age. They were

then tested and it was found that 40% of the controls killed compared

to 0% of the castrates. Didergeorges and Karli (1967) also reported

that testosterone may effect the development of prey killing if com-

bined with some other treatment. For example, these authors found

that castration and adrenalectomy (performed at an early age)

reduced the percentage of non-killers which might have been con-

verted into killers by means of an olfactory deafferentation. How-

ever, it was then found that the subsequent administration of

testosterone would induce killing in these anosmic non-killers.

Thus it appears that a rat's level of testosterone is critical if

it is to be converted from a non-killer into a killer by means of

an olfactory deafferentation. The fact that an olfactory deaffer-

entation in an intact non-killer can markedly increase the tendency

to kill has recently engendered a spate of research (Alberts and

Friedman, 1972; Bandler and Chi, 1972; Bernstein and Moyer, 1970;

Spector and Hull, 1972). This finding has already been mentioned

(see discussion concerned with the genetic basis of predation) and

it will be discussed in greater detail in the sub-section dealing

with stimulus control (Section 2.4b.7).

A related area of investigation has been concerned with the

effects of the physiological changes brought on in the female during

the periods of gestation, parturition and lactation. Observation of

several mammalian species has shown that females will become unusual-
ly aggressive towards their own conspecifics during this period
(Barnett, 1958; Beach, 1948; Hafez, 1962; Moyer, 1968). This
fact led Karli (1956) to speculate that possibly females, who would
not kill under normal conditions, would begin to kill if they were
tested when in the special physiological condition characteristic
of pregnancy. In order to test this hypothesis Karli took proven
non-killers, mated them, and tested their reaction towards mice
shortly before and after parturition. The results Karli obtained
from this experiment were unexpected for rather than kill most females
displayed 'active maternal behaviour'. That is, often a pregnant or
lactating female groomed the mouse during an encounter and at times
it even retrieved it to its nest. In the presence of a litter a
mouse, on occasion, interfered with normal maternal care. That is
to say, it pushed the pups out of the nest and even ate them all in
the presence of the mother !

Karli's results, although surprising and clear cut, nevertheless
left unanswered the question of what effect pregnancy might have on
female rats who were experienced killers before they became pregnant;
it should be remembered that Karli used exclusively non-killers.
Would experienced killers reverse their reaction towards mice during
pregnancy and instead behave maternally like the non-killers did?
Baenninger (1969) addressed himself to this question and the results
from his experiment conclusively showed that experienced mouse killing
mothers continued to kill both before and after parturition. In this
study Baenninger also succeeded in replicating Karli's earlier finding
with non-killing females; like Karli, he too found that lactating

non-killers behaved maternally when confronted with mice.

These studies by Karli and Baenninger demonstrate that mouse killing by rats is independent of the endogeneous states brought on by pregnancy. However, as one might almost expect, some researchers have presented evidence which contravenes this general conclusion. For example, Flandera and Novakova (1971) in their investigation worked with four strains of laboratory rats and found that pregnancy and lactation had no effect on prey killing in three of the strains, but for the rats of the Wistar-SPF strain they obtained positive results. In their experiment mice were presented to females of this strain on the day before mating and on the 1st, 3rd, 5th, 7th, 10th, 15th and 25th day following parturition. Results showed that the incidence of killing was relatively low prior to mating (4.5%) but with the onset of lactation the incidence of killing significantly increased. On the third day after parturition 30% killed and on the fifth day 60% killed. Thereafter the number of rats which killed steadily decreased (30% on the seventh day and 18% on the tenth day) until it reached a level (0% on both the 15th and 25th days) which did not differ significantly from the level prior to mating. Mothers which killed on the fifth and seventh days of lactation (i.e. at the time when their mouse killing was at a peak) were also tested on the same day in a novel environment without the presence of their pups. It was found that these subjects continued to kill, thus indicating that it was the unique hormonal state that the female was in which induced her to kill and not the mere physical presence of the pups.

Endroczi, Lissak and Teledgy (1958) also found that frog kil-
ling was specific to the lactating mother. These authors reported
that only the lactating mother in the presence of her young would
kill; neither male rats nor non-lactating females showed this
behaviour. However, contrary to the results of Flandera and Novakova
these authors found that lactating females separated from their litters
and tested in a novel environment would not kill.

Further conflicting results come from the study of Relvis and
Moyer (1969) who attempted to replicate the findings of Endroczi et
al. and failed. What Relvis and Moyer found was that lactation and
the presence of the pups did not serve to increase the incidence of
frog killing; instead, lactating females, like the females in Karli's
and Baenninger's experiments, tended to behave maternally towards
them. Moreover, Relvis and Moyer found that a significant number of
naive virgin females killed frogs, thus again suggesting that a female
did not have to be in the unique hormonal state characteristic of
pregnancy in order to kill.

On the whole this area of research is largely characterised
by a paucity of data which at times are conflicting. Apparently the
only studies to date concerned with the effects of testosterone are
those of Karli (1958), Didieregeorges and Karli (1967) and Baenninger
and Ulm (1971). Certainly more research is needed before any
definitive conclusions are drawn. Very generally, though, one
might tentatively conclude that the male hormone testosterone, which
plays a large role in intra-specific aggression, has only a marginal
influence on a rat's prey killing tendencies. Probably the most

consistent finding which has emerged from the studies concerned with

a lactating female's response is that a female if she does not kill

will usually behave maternally towards the prey. This has been found

with mice (Baenninger, 1969; Karli, 1956) as well as with frogs

(Relvis and Moyer, 1969). The reason why some results conflict

with this finding are at the moment obscure; however, they could

be due to the fact that different strains have been used in the var-

ious experiments or possibly because not all of the experimenters

have tested their subjects with the same type of prey; i.e. some have

used, mice and others frogs.

2.4b.6. The Motivation of Predatory Behaviour

Functionally it is not difficult to discern the value of

predatory killing; the behaviour in all likelihood is primarily

concerned with food procurement. Labelling it as a 'food getting'

behaviour seems quite appropriate (Denny and Ratner, 1970) for it

is known that even laboratory predators will eat the prey following

a kill if given the opportunity. For example, experienced rat

killers will eat the frogs and mice they kill (Bandler and Moyer,

1970; Paul, 1972; Paul and Posner, 1973; Thorne, Aaron and Latham,

1973) and likewise cricket killing by mice is often followed by

consumption (Thomas, 1969, 1972). Because of the obvious functional

value and because of the close sequential relationship between killing

and eating one might well conclude that these two events were related,

or one caused the other, or perhaps even be tempted to hypothesise a

direct relationship between the tendency to kill, the tendency to feed and predator's level of hunger.

However, as might be expected, the relationship between the killing of prey, the consumption of it, and hunger is not as straight-forward and simple as it might hypothetically seem. To understand this, take first the case of the animal who has had some prior exper-ience with the prey. This experience need not only mean the experinece of a successful kill but also the experience of not killing even though the prey was readily available. For such animals it seems as though the motivation to kill is independent of the need for food or the tendency to feed. This belief is supported by the following obser-vations:

1) Predators have been known to kill far more prey than they need in order to satisfy their food requirements. Such surplus killing has been documented in the order Carnivora by Kruuk (1972b) for canids and hyaenas, by Schaller (1972) for felids, by Rasa (1973) for viverrids, and another good example of killing in surplus can be found in the raids and killing 'orgies' by certain canids on domestic livestock. In the order Rodentia, Boice and Schmeck (1968) reported that the carnivorous grasshopper mouse will kill up to 40 crickets within a period of two hours and DeSisto and Huston (1970) noted that domestic rats will kill as many as 30 frogs in rapid succession. Pres-umably then, predators are capable of killing far more prey than they could eat or would need to eat in order to satiate their hunger drive.

2) <u>Prey killing will remain stable and constant in form even</u> <u>if a predator is denied the opportunity to feed on the prey which it</u> <u>has killed.</u> Myer (1967, 1969, 1971) has repeatedly demonstrated this in several of his studies with mouse killing rats. According to Myer the act of killing is self-reinforcing in itself and reinforcing a rat by allowing it to feed on the mouse is not necessary in order to maintain the behaviour. Leyhausen (1973) also noted that "once established the killing bite will continue to develop its own appetite" (p-243).

3) <u>Experienced non-killers cannot be induced to kill through</u> <u>starvation.</u> For example, Karli (1956) found that rats which never killed mice could not be made to do so even if subjected to extreme food deprivation. In fact, Karli reported that some of his rats starved to death in the presence of the prey. Likewise, Kuo (1930) in his study with cats reported that hunger had little effect on the rat killing response of non-killers.

4) <u>A predator after its first few kills may not consume the</u> <u>prey which it has killed.</u> Paul, Miley and Baenninger (1971) reported that, initially, rats occasionally showed hesitancy about eating the prey. Karli (1956) also found that after the first few kills rats tended not to eat the mice or eat only after a great delay. With deer mice, Thomas (1971) found that the interval between killing and eating was often several minutes. Moreover, Leyhausen noted that consumption of the prey does not automatically follow a kill. According to Leyhausen a predator has to learn the 'connection' between killing and eating. Therefore, it seems that these two

behaviours are unrelated at first but subsequently become sequentially linked through the process of association.

5) <u>Several variables which influence the probability of eating have been found to have little effect on prey killing</u>. For example, it is well known that whether hungry or not an experienced mouse killer will kill if given the opportunity (initially Karli, 1956, and since then many others). Further, Paul, Miley and Baenninger (1971) reported that water deprivation had little influence on the incidence of mouse killing (if thirsty the probability of mouse killing should be low as it is with eating) and subsequently Paul (1972) found that the severity of food deprivation (75% <u>ad lib</u> feeding weight) and the time of testing in relation to the regular feeding hour (consumption of food and the probability of eating are highest at an animal's regular scheduled feeding time) had negligible effects. If killing and hunger were related then a rat should be more likely to kill the hungrier it was and also if it was tested at the time it regularly fed.

6) <u>The act of killing does not potentiate prey feeding</u>. If killing and feeding were related then a predator should show a greater inclination to feed on prey which itself had killed as opposed to prey which it had not killed. However, Paul and Posner (1973) found that rats presented dead prey which they themselves had not killed were just as likely to feed on such prey as those rats who were allowed to feed on prey which they themselves had killed. Further, the act of killing does not signal to serve as a cue to the predator to begin eating the prey which it has killed. Rats given the choice

between a piece of chocolate and the prey immediately following a

kill were just as likely to eat the chocolate as they were the prey

(Paul and Posner, 1973).

7) Different anatomical sites in the brain govern eating and

killing. For instance, King and Hoebel (1968) reported that electric-

al stimulation in several sites of the rat's hypothalamus would elicit

killing but not eating. In the study of Panksepp (1971a) the reverse

was found; i.e. stimulation which elicited eating would not elicit

killing. In addition, it has been reported that stimulation of a

rat's lateral hypothalamus will produce intensive oral activities,

which resemble eating, but never attack and killing (Karli, Vergnes

and Didiergeorges, 1969). In another study, using cats, Hutchinson

and Renfrew (1966) found that although attack and killing could be

elicited from the same hypothalamic sites different intensities were

required for each of the behaviours; attack required more intense

stimulation for its elicitation than did eating.

Further, an intensive research programme by Flynn and associates

(reviewed in Flynn, 1967, or Flynn, Venegas, Foote and Edwards, 1970)

has produced conclusive evidence indicating that attack, killing and

feeding are neurophysiologically distinct. Granted, Flynn argued,

the findings of Hutchinson and Renfrew (cited above) are correct in

that they substantiate the fact of definitive areas within the hypoth-

alamus which when stimulated will elicit both attack and feeding. How-

ever, according to Flynn, they still do not obviate the likely possibil-

ity that different sites may also be involved. Like several others he

draws on evidence which shows that stimulation to a particular hypoth-

alamic site, known to elicit attack and killing, will not elicit

feeding. Five examples are presented to support this contention.

First, he cites one of his early studies (Wasman and Flynn, 1962)

in which cats were stimulated in a hypothalamic area known to reliably

elicit attack, but only in the presence of a dish of food (no prey was

present). Under these circumstances Flynn found that his cats would

sniff at the food, savagely bite it and then prowl around the cage

(apparently, in an appetitive search for the prey) with the food often

falling out of the mouth. In no instance was the food ever ingested.

Second, Flynn found that if stimulation which elicited attack was

prolonged beyond the attack itself then this would not induce a cat

to start feeding on the prey. The underlying assumption of this

finding was that if killing and feeding were related neurophysiolog-

ically, then the same site which elicited killing should likewise have

elicited eating. Third, Flynn reports an experiment in which cats

were presented either horsemeat or anaesthetised rat concomitant with

stimulation to several selected sites in the hypothalamus at different

levels of intensity. The intensity of stimulation in this experiment

was raised in increments until a subject either ate the horsemeat or

attacked the rat. Flynn found, in five of his seven cats tested, that

stimulation which elicited attack would not elicit feeding. Moreover,

the more intense the stimulation was (it ranged from .10 to .60 mA) the

more readily attack was elicited, and in the two subjects in which

attack and eating were elicited from the same sites, more intense

stimulation was needed to elicit eating than attack. Fourth, Flynn

cites an experiment in which cats were stimulated both in the presence

of horsemeat and a rat. During all presentations, however, the food

was always placed closer than the rat to the cat for it was known
from previous research (Hutchinson and Renfrew, 1966) that whether a
cat would attack or feed depended to an extent on which object was
closer. Thus, in this situation, with stimulation to the same site,
one would have expected most cats to eat rather than attack, assuming
that attack and eat were both under control of the site being stimu-
lated. However, the results clearly showed that rather than eat most
cats attacked. Lastly, Flynn notes that if cats were continuously
starved for three days, then given food, and then shortly after a rat,
they would break off eating to attack the rat when stimulated. Taken
together the evidence drawn from these five examples suggests that
stimulation in certain sites in the hypothalamus will evoke predatory
attack but not eating.

Additional weight for the theory of separate neural centres for
killing and eating has come from the research of Karli and associates
(cited in Karli, Vergnes and Didiergeorges, 1969). These authors
claimed that they successfully abolished both eating and killing in
rats with bilateral lesions in the hypothalamus; however, they sub-
sequently found that the recovery of killing invariably preceded the
recovery of eating. According to these authors, "the question arises
as to whether or not hunger or some selective appetite are essential
factors in building up the motivational state underlying the killing
response. We feel that this is not the case for the following reason:
if the animal bearing lateral hypothalamic lesions.....recovers oriented
behavioral activities, the recovery of the killing response invariably
preceded....the recovery of the feeding behavior: the reappearance of

interspecific aggression may thus occur even though the animal

still happens to be in a state of complete adipsia and aphagia, never

eating anything of the mouse it kills." The interested reader should

consult Roberts and Kiss (1964) for additional evidence that different

anatomical sites in the brain govern the eating and killing responses.

Thus, what the evidence reviewed so far suggests is that prey

killing in the experienced predator is governed by a motivation which

is separate and distinct from the motivation which governs feeding.

This being the case a number of investigators have reported experi-

ments which show that the act of killing itself can serve as a rein-

forcer. Kilby, Moore and Harris (1973) and Myer and White (1965),

for example, have demonstrated that the opportunity to kill mice or

frogs was a sufficiently strong incentive to maintain discrimination

learning by rats. In both of these studies rats who were experienced

killers learned to enter the arm of a T-maze that led to prey which

they could kill. In similar fashion, Roberts and Kiss (1964) reported

that cats during stimulation of the hypothalamus learned to enter the

arm of a Y-maze in order to gain access to a rat which they could kill.

Rats have even been taught the operant response of bar pressing in a

Skinner box for the delivery of a reward - a mouse which could be

killed (Van Hemel, 1972; Van Hemel and Myer, 1970) or a frog which

could be killed (DeSisto and Huston, 1971; Huston and DeSisto, 1971).

If the act of killing is reinforcing in its own right and further

have motivational properties of its own then one would eventually

expect the behaviour to satiate after it has been performed so many

times. Kulkarni (1968a) has gathered evidence which shows that this

is in fact what happens. In his experiment three groups of twelve

experienced killers were presented seven mice in succession at inter-

vals of 15, 30 or 60 minutes, respectively. Kulkarni found that half

the rats in the 15 minute group stopped killing during testing as

opposed to only three in the 30 minute group and only one in the 60

minute group. Thus, whether or not a rat stopped killing seemed to

depend on the interval between presentations. Kulkarni argued that

the waning of mouse killing was due to the exhaustion or habituation

of the behaviour and he used the term action specific exhaustibility

to explain his findings.

Additional evidence along these lines has come from Moyer (1971)

who found that the killing behaviour of an experienced rat killer

would satiate if it was presented between five and ten mice in suc-

cession at intervals of one minute each. Moyer observed that when

this occurred a satiated rat would allow an exploring mouse to walk

over it and even nestle with it. Further, Moyer notes that a rat's

tendency to kill frogs also waned after its mouse killing behaviour

had satiated, thus suggesting that both the killing response to

frogs and mice were governed by a similar motivation.

Up to now the discussion has been solely concerned with those

animals who were regarded as 'experienced'; that is, experienced

in terms of killing or not killing. This distinction was necessary

for it helps to explain some important data recently collected by

Paul and colleagues (Paul, 1972; Paul, Miley and Baenninger, 1971).

What these authors found was that food deprivation served to

facilitate the initiation of mouse killing in naive rats. Hunger, in one study (Paul, Miley and Baenninger, 1971) was induced through a two week period of cyclic food deprivation prior to the initial mouse killing test and in another study (Paul, 1972) through continuous starvation for seven days. In fact, it was found that just the experience of being maintained on the cyclic schedule (and later tested when food satiated) increased the chances of killing considerably. These findings are important and above all reliable for they have been replicated by these authors in a series of experiments (also see Paul, Miley and Mazzagatti, 1973).

At first they may appear discrepant with the earlier cited work and especially with the finding of Karli (1956). However, Paul and her colleagues argue that if one attempts to explain the differential effects of starvation in terms of the past experience of the animal being starved then their findings do not conflict with Karli's. Karli, they assert, exposed his rats to the potential prey both before and during the course of food deprivation while in their experiments rats were first exposed to the mice only after a substantial period without food. Accordingly, then, such prior experience interfered with subsequent killing when the rats were quite hungry (Paul, 1972). More to the point, what is inferred is that the prior exposures Karli's animals received (when they were food satiated) reinforced habits incompatible with killing, or simply strengthend the habit of not killing per se. These habits, in turn, interfered with and suppressed whatever potentiating effects starvation might have had.

Paul (1972) conducted an elegant experiment to test this hypothesis. Rats (all naive) were assigned to four groups and housed either individually, or with the prey species, a single mouse. Further, half the rats in each group were continuously starved for seven days prior to the first mouse-killing test, or maintained for seven days on a cyclic feeding regimen. Thus, half the rats were exposed to the prey during the course of starvation and half were not. When tested those subjects who were housed with the prey killed in significantly fewer instances compared to those subjects who were starved but without such exposure. Moreover, rats from both the exposed and the non-exposed groups which were continuously starved showed a greater incidence of killing than those subjects which were maintained on the cyclic schedule. Further Paul let all subjects feed ad lib for three days following the last moust killing test. They were then subsequently tested and it was found that every rat which killed when hungry continued to kill when food satiated. Thus, hunger did not seem to be a necessary condition to maintain killing initially induced through starvation.

Evidence suggesting some relationship between feeding and killing has also come from the work of Paul and associates (see Paul and Posner, 1973). In one experiment these authors starved naive rats for four days and then proffered to them a dead mouse (killed by another rat) which they were allowed to feed on for 30 minutes. Mouse killing tests were then conducted 30 minutes later and compared to those of rats who were tested first without prior eating. These eat-first subjects showed a greater incidence of killing (76% vs. 51%) and killed with a significantly shorter latency. This finding thus suggests that eating dead prey potentiates killing in the naive

predator.

In summary, the evidence reviewed in this section suggests
that a subject's past experience with the prey is of paramount
importance in determining the effects hunger and prey feeding have
on the predatory response. It seems that these two variables have
relatively little influence on the maintenance of killing in the
experienced killer but, on the other hand, a positive influence on
the initiation of killing in the naive subject.

The fact that prior dead feed has positive consequences and
that the drive for killing and that of hunger become separate through
experience makes sense biologically speaking.[29] Feeding on dead prey
or partially killed prey brought in by the mother could be one means
by which the young inexperienced predator familiarizes itself with
novel prey. Prey killing responses could then be practiced and the
young predator could learn that what it was feeding on was in fact
an edible and palatable food substance. Observations do in fact
substantiate the belief that a mother often assists in introducing
the young to their first prey; this happens, for example, in domes-
tic cats (Ewer, 1968a), tigers (Schaller, 1967), cheetahs (Eaton,
1970; Kruuk and Turner, 1967) and grasshopper mice (Ruffer, 1966).

The fact that an experienced predator will continue to kill

---

29. In the more specialized predators, such as Carnivora, experience
    may not be needed to separate out the killing and hunger drives.
    Due to the selective pressures placed on the killing response
    in those species who depend primarily on prey as a source of
    food, it is conceivable that the killing drive has become
    emancipated from the hunger drive. Lorenz (1966), Leyhausen
    (1973) and other ethologists have argued strongly for this point.

even though it may not be hungry is one means by which it could

assure itself, or its companions (in the case of group-living predators),

of an adequate supply of food. Prey which was not eaten after the kill

could be passed on to a conspecific or cached for later consumption.

The sharing of prey could be a means of maintaining organization within

a social group and caching could prove advantageous to predators who

hibernate or to predators who do not have access to the prey the year

round (see Ewer, 1968, pp. 54 - 55 for a brief discussion on this point,

or see Kruuk, 1972b).

Lastly, another shortcoming of the majority of studies reviewed

in this section stems from the fact that most researchers have assumed

that hunger is a unitary concept when in fact it is not (Deutsch,

1971). Many specific hungers exist (Rozin and Kalat, 1971) and it

could well be that a rat, for example, who is apparently well-satiated

on laboratory chow still has a specific hunger for mice (or perhaps

some specific part of a mouse, such as the brain); hence it could be

just this type of hunger and not hunger in a general sense which drives

it to kill. The fact that eating often follows a kill in the predator

satiated on laboratory chow certainly suggests that a specific hunger

may be present; however, few researchers have taken this variable into

account as a causal factor. Because of this addition research is

needed to ascertain if a specific hunger for mice (or frogs) exists

and if so what effect it has on the killing response. Until then one

must remain somewhat sceptical of any theory concerned with the rela-

tionship between hunger, prey feeding, and killing, or on the motivation

for killing in general.

2.4b.7.   Stimulus Control of Predation

The investigator can approach this area of research in two

basic ways; either he can alter the stimulus characteristics of

the prey or, alternatively, eliminate the sense modalities of the

predator. Both approaches are complementary and each ultimately will

answer questions about the stimuli which control the predatory res-

ponse. The investigator can adopt the first method and alter, for

example, the odour of the prey and depending on the results he

could conclude whether or not a predator depended on its sense of

smell for the release of its attack and killing. If the results

showed that a predator continued to kill after the odour of the

prey was camouflaged then it would be safe to say that olfaction

played a minimal role in the control of the behaviour. On the other

hand, the investigator could approach this problem of stimulus con-

trol with the second method and perhaps surgically remove a predator's

olfactory bulbs or even sever its olfactory tracts, thus rendering

it anosmic. If killing continued under these conditions then a

conclusion similar to the one above might be drawn. Thus, in general,

the investigator has at his disposal two basic methods with which to

determine what stimuli control the predatory response.

Only a handful of studies have directly embarked on questions

concerned with stimulus control and, needless to say, most of these

have involved the white rat. Karli (1961) showed that successive

removal of a rat's olfactory bulbs and vibrissae, or blinding and

deafening, did not eliminate mouse killing in established killers.

Myer (1964) also reported that rats who were experienced killers

would continue to kill even if they were deprived of their visual,

olfactory and tactile senses. Due to his findings Myer concluded

that killing by experienced mouse killers was under multi-sensory

control.

However, Myer, in his well known study, mainly addressed

himself to the question of why mouse-killing rats would never kill

rat pups. The failure to kill rat pups obviously puzzled Myer for

physically they were very similar to mice and further he knew that

rats which killed mice would also kill other small rodents, such as

gerbils and hamsters. With these considerations in mind, Myer

hypothesized that the pups probably possessed the stimuli required

to elicit attack and killing but, at the same time, they also prob-

ably possessed some unique olfactory characteristic which inhibited the

response. To test this hypothesis Myer employed both methods that

were outlined at the beginning of this section; more specifically,

he felt that if he could alter the odour of the pups or possibly

eliminate the rat's ability to perceive them then, perhaps, he could

disinhibit the rat's pup killing response.

In his experiment Myer selected for use subjects who had con-

sistently killed mice but not rat pups. The first phase of the

testing regime consisted of presenting subjects stimulus animals

that had been altered in the following ways: 1) a perfumed rat pup;

2) a rat pup sealed in a transparent airtight envelope; 3) a pup

sealed in a perforated transparent envelope; 4) a pup that had been

previously housed with mice, and lastly 5) a pup coated with mouse

urine. The results Myer obtained provided strong support for his

hypothesis; rat pups whose odour had been masked with perfume were killed in all instances and pups that were sealed in airtight envelopes were killed nearly three-quarters of the time. Subjects in the control group, i.e. pups sealed in perforated envelopes were never killed at all. Pups previously housed with mice and pups coated with mouse urine elicited killing in only a few instances; apparently altering pups in this way did not produce a great enough olfactory change to induce pup killing in these mouse killers. In the second phase of the experiment these same subjects were either blinded or rendered anosmic;. this was accomplished by removing their eyes and olfactory bulbs. They were then tested with the same type of altered pups that they had previously been tested with. Again the results unequivocally supported the hypothesis that the odour of the pups was the factor preventing pup killing. For example, anosmic rats killed pups in all instances; moreover rats that were just blinded continued to kill altered pups (e.g. pups bathed in perfume or pups sealed in airtight envelopes) but not unaltered ones, thus indicating that a rat's vision played a minimal role in the control of its pup killing behaviour.[30]

The experiments cited so far have shown what stimuli are opera-

---

30. Since this investigation by Myer pup killing has become a research topic in its own right. It has been found that rats, mice and hamsters will kill and eat pups of their own species (Gandelman, 1972, 1973; Gandelman, Zarrow and Denenberg, 1971; Gandelman, Zarrow, Denenberg and Myers, 1971; Noirot and Richards, 1966; Rosenberg, Denenberg, Zarrow and Frank, 1971). If cannabilism is predatory is debatable. However, whatever the case, the literature on this topic will be excluded from this review on the grounds that it does not fit in with the definition of predatory behaviour provided in Section 2.1.

tive in the control of mouse killing reaction and for that matter

the pup killing reaction as well. Reflecting on these findings it

is important to realise that they are based on experiments in which

experienced killers were exclusively used; hence they shed no light

on the stimuli controlling the reaction of the inexperienced killer.

It is possible that after a predator has acquired some killing exper-

ience it comes to respond to cues which initially did not cause any

reaction at all. For example, when a naive rat first encounters prey

its initial attacks, conceivably, could be elicited solely by move-

ment (of the prey) but with experience it is likely that it could

come to learn to associate movement with the sight or even with the

smell of the prey; hence, with experience attack and killing could

come under the control of several stimuli. This, in fact, could well

account for Myer's conclusion that mouse killing by rats was under

multi-sensory control.

Even though there is no hard core experimental evidence at

present to support the above hypothesis, there is, however, an

abundance of evidence which suggests that movement (of the prey)

is the omnipotent releaser of attack behaviour in a number of mammal-

ian predators. Kreiskott (1969), for example, reported that a naive

rat's attack latency would be unusually long if it was confronted with

inactive mice; prey like this usually elicited prolonged exploratory

behaviour, grooming and other types of social behaviour but never

attack. Likewise, Panksepp (1971a) reported that some rats would

attack moving mice but never dead ones. With grasshopper mice, Horner,

Taylor and Padykula (1965) reported that their subjects, when given

the choice between a moving versus an immobile insect, invariably

selected the moving one. Certain marsupial species also respond strongly to movement. Ewer (1968b), for example, describes how a marsupial mouse came across a cricket which merely walked slowly at first; consequently it was ignored. However, it was immediately attacked the moment it hopped. Ewer also notes that her marsupials only took moths which fluttered; moths which did not flutter were usually ignored. More dramatically she even claims that her animals attempted to seize flying insects out of the air.[31] The polecat also seems to be extremely responsive to movement. For example, Eibl-Eibesfeldt (1961) reported that a naive polecat before it would attack had to be confronted with moving prey; motionless prey usually elicited exploratory and grooming behaviour. In the canid family the story also seems to be the same. For example, Fox (1969, 1971) noted that prey movement released orientation and approach in a number of species (the wolf, coyote, fox and dog). If these predators were confronted with motionless prey they would often stab at it with their forepaws or pick it up in their mouths and throw it in order to simulate movement.

The fact that a predator's attack is so largely contingent upon movement is not surprising for it is well-known that movement of the prey is a necessary condition for the release of predation in a wide range of vertebrate species (Marler and Hamilton, 1966). Moreover, it should be recalled that the inverse of movement, namely immobility

---

31. Ewer uses these examples to support the notion that her mice possess an innate disposition to attack anything small which moves.

or freezing, is one of the chief protections prey have against

predators (see Section 2.4a). Obviously then, prey take advantage

of the fact that their movement is a necessary condition for the

release of their adversary's attack.

Neurophysiological research has also been concerned with the

stimuli which release predatory attack and killing. For example,

MacDonnell and Flynn (1966) eliminated several sense modalities of

the cat (the eyes were wrapped with gauze and the olfactory bulbs

ablated) and then applied electrical stimulation to the hypothalamus

in order to elicit killing.[32] They found that vision and tactile cues

from the cat's forepaws and muzzle were the main senses employed in

prey location; olfaction played a relatively unimportant role. Once

the prey was located these electrically stimulated cats killed in the

normal feline manner; i.e. with a bite to the nape of the prey's

neck.

Another line of neurophysiological research has stressed the

specificity of the stimuli which elicit attack and killing. In the

study of Wasman and Flynn (1962) cats were stimulated in the hypoth-

alamus and then given a choice of objects to attack. The cats pre-

ferred to attack a live rat rather than a dead rat and either one

to a stuffed rat or stuffed dog. In another experiment Levison and

Flynn (1965) gave cats the choice between an anaesthetized rat, a

---

32 . Electrical stimulation of the brain was necessary because the
cats in this study were non-killers. However, it was known
that they would kill if stimulated in the appropriate brain
region. The fact that most laboratory cats are non-killers
has already been mentioned (See Section 2.4b.4).

stuffed rat, a small hairy toy dog, a rubber foam block or a styro-
foam block and found that most cats attacked the stuffed or anaesthet-
ized rat rather than the other three stimulus objects. In addition,
these authors found that the attacks directed to the anaesthetized
rat were more persistent than those directed to the stuffed rat or
hairy dog.

With opossums comparable results have been reported. For
instance, Roberts, Steinberg and Means (1967) simultaneously pres-
ented to their subjects a live rat, a dead rat, a shoe and a wooden
block and found that the opossums spent significantly more time
attacking the live rat as opposed to the dead rat, shoe, or wooden
block. Further, these authors reported that attack only occurred
if the goal object was present during stimulation; if absent the
opossums explored the test arena. Thus this indicated "that the
stimulation was not eliciting the overt behaviour directly or auto-
matically, but was enhancing the capacity of the goal object to
elicit the responses" (p-11).

Rats also seem to be selective in the prey which they attack.
For example, DeSisto and Huston (1971) presented their subjects sev-
eral objects during hypothalamic stimulation and found that the rats
attacked a live frog on 64% of the trials, and a dead frog, rubber
mouse and live mouse on 26%, 10% and 0% of the trials, respectively.
Moreover, Bandler and Moyer (1970) have demonstrated that rats natur-
ally show a preference for certain types of prey (i.e. without the aid
of brain stimulation). For example, they found that rats preferred to
attack frogs and chicks as opposed to mice and turtles. However,

these authors further discovered that the prey most preferred (i.e.
frogs and chicks) were not necessarily the prey most capable of
eliciting attack (frogs and turtles elicited more attack than chicks
and mice).

The research reviewed above shows that attack and killing in
rats, cats and opossums is elicited most readily by certain classes
of stimuli. Because of such specificity some authors in their writ-
ings have come to refer to attack behaviour as 'stimulus bound'
(King and Hoebel, 1968; Panksepp, 1971a, 1971b, 1971c; Panksepp and
Trowill, 1969); in other words, this term is a short way of saying
that attack behaviour is <u>bound</u> to certain key stimuli emanating from
the prey object(in addition to the effects of brain stimulation).

Up to now the discussion in this section has been mainly con-
cerned with the stimuli which facilitate predatory attack. It has
been concluded that movement of the prey is of paramount importance
but eventually the response could come under the control of several
stimuli. On the other hand there are also those stimuli which seem
to inhibit attack behaviour. We know that Myer (1964) felt that it
was the odour of the rat pup which inhibited the adult rat from
attacking it and recently Avis and Treadway (1971) have come forth
with evidence which suggests that mouse killing itself may be inhib-
ited by the odour of the mouse.

In their experiment these authors selected for use rats which
rapidly and reliably killed mice in their own home cage. Subjects
were then subsequently tested for killing after being transferred into

one of the following cage conditions: 1) a cage in which another rat had previously lived; 2) a cage in which several mice had lived and 3) a freshly cleaned neutral cage. Results showed that 80% of these experienced killers stopped killing when tested in the cage in which mice had previously lived. A significantly greater number killed when tested in the rat soiled cage or neutral cage. Avis and Treadway thus concluded, "olfactory cues play a role in inhibiting rat-mouse aggression" (p-294).

.Unfortunately this conclusion must be treated with circumspection for several reasons. First, Bandler and Chi (1972) have gathered evidence which runs directly counter to it. What these authors found was that both frog killing and mouse killing in the experienced killer could be suppressed through bilateral bulbectomy. Thus, if the odour of the mouse was the factor inhibiting mouse killing, as Avis and Treadway's data suggested, then one would have expected bulbectomy to have no effect, or at best a facilitory effect, rather than an inhibitory effect. However, as stated, the finding of Bandler and Chi decidely contravenes this expectation.

Second, some authors have seriously questioned the premise of the assumed relationship between olfaction and prey killing. As previously noted both Karli et al. (1969) and others (see discussion and references in Section 2.4b.4) have consistently found that olfactory bulb removal would induce killing in non-killers. Basically it was assumed in most of these studies that through such treatment a non-killer became insensitive to the odour of the prey and because of this its mouse killing behaviour became 'disinhibited'; consequently

this caused it to kill. Naturally, the underlying assumption of this research was that some olfactory property (presumably from the mouse) inhibited killing. However, this assumption no longer seems tenable because of recently marshalled evidence which strongly indicates that it is not anosmia per se which causes the bulbectom-ized non-killer to kill, but rather mouse killing is induced through some side effect of the bulbectomy operation itself. The research teams of Alberts and Friedman (1972) and Spector and Hull (1972) deserve credit for this important discovery, although Karli et al. (1969) did express some earlier scepticism on this matter.

In their paper which appeared in Nature, Alberts and Friedman assert that the bulbectomy operation in general presents "interp-retive difficulties because it may be erroneous to identify loss of olfaction as the sole cause of behavioural alterations after bulb-ectomy" (p-454). More simply stated, these authors argued that the bulbectomy operation besides removing the olfactory bulbs also results in other structural damage to the brain (specifically in the limbic system) and it is this and not anosima which causes the non-killer to kill.

To test this hypothesis Alberts and Friedman took proven non-killers and rendered them anosmic through the peripheral means of injecting zinc sulphate internaslly; hence, anosima was accomplished with the assurance of no possible structural damage to the central nervous system. Subjects in this group were then tested for mouse killing and the incidence of killing in this group was compared to that of three other groups of non-killers who underwent either one

of the following treatments: 1) the standard bulbectomy operation;

2) a sham bulbectomy operation; 3) saline solution injected internaslly

(rather than zinc sulphate). The results showed that 53% (16 of 30)

of the bulbectomized rats killed post-operatively as opposed to 10%

(3 of 30) of the zinc sulphate treated rats, 10% (2 of 20) of the sham

operated rats and 0% (0 of 20) of the saline treated rats. Further,

the difference among the groups was highly significant ($p < .001$).

In short, this experiment showed that it was olfactory bulb removal

and not anosmia which induced mouse killing in the non-killer. This

finding led Alberts and Friedman to conclude, "rats rendered anosmic

by intra-nasal zinc sulphate and bulbectomized rats are behaviourally

disparate and that the destruction of the central nervous tissue, not

anosmia, seems to mediate.....mouse-killing behaviours exhibited by

bulbectomized rats"(p-454).

Independently, Spector and Hull (1972) reached basically the

same conclusion although through a slightly different means. Rather

than inducing anosmia by means of zinc sulphate these authors rendered

their rats peripherally anosmic through the surgical destruction of

the receptor cells in the snout (referred to by these authors as

'deafferentation'). Briefly, the breakdown of their experiment was

as follows: All rats were previously screened as being non-killers

and then administered either one of the following treatments:

1) the deafferentation treatment (specifically this consisted of

the destruction of the nasal mucosa and fila olfactoria) with the

bulbs left intact; 2) bilateral removal of the olfactory bulbs and

3) neither bulb removal or deafferentation. When tested post-operatively

mouse killing occurred in 80% (4 of 5) of the bulbectomized rats,

0% (0 of 10) of the deafferented rats and 0% (0 of 3) of the control

rats. In summary, these results showed that pure anosmia produced

by deafferentation had negligible effects on mouse killing; that is,

non-killer rats could not be induced to kill through this treatment.

On the other hand anosmia produced by olfactory bulb removal had a

profound facilitory effect. Thus these results again lend support

to the belief that bulbectomized non-killers kill not because they

are anosmic but because of some other inevitable consequence produced

by the bulbectomy operation.

But just what is the other inevitable consequence? More

specifically, if it is not anosmia which induces the non-killer to

kill, then just what is it? Karli et al. (1969) hypothesized that

it was due to the "suppression of an active inhibition previously

mediated through the olfactory pathways" (p-51). Bandler and Chi

(1972) are in general agreement for they write, "the induction of

mouse killing by olfactory bulb removal is not simply due to the

rat's failure to recognize the mouse. This and other data have led

to the suggestion that the mouse killing produced by bulbectomy may

be the result of the release, from an active olfactory inhibition,

of brain sites associated with the excitation of interspecific

aggression" (p-210).

Thus, it is feasible to envisage the olfactory bulbs as being

part of some non-olfactory neural network which acts to inhibit the

mouse killing response. Moreover, it stands to reason that the

disruption (through surgical means) of any part of this network should

disinhibit killing. This in a nutshell is the theory that has been

stressed by virtually all of the researchers in this area and

several experiments have already been reviewed in this chapter

which show that this in fact is what happens.

Spector and Hull go one step further and specifically postu-

late a non-olfactory limbic function for the olfactory bulbs.[33]

According to these authors it is the limbic system which mediates

the inhibition to kill mice. Further, these authors note that the

olfactory bulbs have both direct and indirect neural connections

with several parts of the limbic system. For this reason they

believe that the bulbs should be regarded as being part of it.

Thus, these authors maintain that within the limbic system there

exists some sort of inhibitory pathway, and since the bulbs are

part of the system they they can be viewed as subserving a non-

olfactory function in addition to an olfactory one.[34]

Before leaving the topic of bulbectomy and induced killing

two other valuable findings need mentioning. First, it seems

unlikely that the killing response induced through bulbectomy is

a genuine form of predatory behaviour. Bulbectomized rats typically

attack and kill in a disorganized savage-like manner with obvious

---

33. Broadly speaking, the limbic system seems to be the neural
substrate for behaviour related to motivation and emotion.
Often it has been referred to as the 'old brain', 'smell
brain' or 'nose brain' due to the involvement it has with
various olfactory functions. Structures within the limbic
system include the thalamus, hypothalamus, amygdala, cingulum
and septal region (Johnson, 1972).

34. According to Spector and Hull: "the pathway and termination
points of this inhibitory pathway are unknown, but the vent-
romedial hypothalamus, amygdala and cingulum are likely to
be involved" (p-356).

signs of emotional rage (Alberts and Friedman, 1972; Bernstein and Moyer, 1970; Kumadaki, Hitomi and Kumada, 1967; Spector and Hull, 1972). Behaviourally it is entirely different from the unemotional, efficient and stereotyped killing response exhibited by natural killers. These two modes of killing have been respectively labelled as 'affective' and 'quiet-biting' attack (Panksepp, 1971a). Because of this difference Bernstein and Moyer (1970) have argued that mouse killing produced by bulbectomy is more closely related to irritable aggression than to predatory aggression. The fact that bulbectomy often produces a generally irritable and hyperemotional rat has been documented by many investigators (Alberts and Friedman, 1972; Bernstein and Moyer, 1970; Douglass, Isaacson and Moss, 1969; Kumadaki, Hitomi and Kumada, 1967; Malick, 1970)

Second, the outcome of the bulbectomy operation in the natural non-killer probably depends on several other factors such as the genetic background of the rat (rats selectively bred for killing are more responsive to this type of operation than rats randomly bred) and the conditions of the post-operative environment into which the bulbectomized rat is housed (rats housed in social isolation are more responsive than those who are socially housed, Karli et al. 1969).

In drawing this section to a close we may conclude that bulbectomy may either facilitate or inhibit a rat's prey killing response. Whether or not it acts in a facilitatory or inhibitory manner seems

to depend on both genetic and experiential factors. As noted above
Karli et al. reported that an animal's genotype could influence the
outcome of this operation and preceding this evidence was reviewed
which showed that bulbectomy could, on one hand, inhibit the killing
of experienced killers and, on the other hand, facilitate the killing
of inexperienced killers.

2.4b.8.   Areas for Future Research[35]

By now it should be apparent to the careful reader that the
research reviewed has fallen into one of the following categories:
1) basic behavioural patterns;   2) the development of predatory
behaviour;   3) hormones and predation;   4) the motivation of preda-
tion and 5) the stimulus control of predation.   Although these are
the main areas researchers have concentrated on they still by no
means are indicative of all the work that has been done in this
field.

For example, the excellent research of the ethologists has been
hastily discussed.   The contributions of Leyhausen and the field
studies of Kruuk constitute some of the best all-round work by
ethologists on mammalian behaviour in general.   Second, most of the
research on the neurophysiology of predation has been neglected.
The interested reader should consult Karli, Vergnes and Didiergeorges
(1969) or Moyer (1968) for a review of this literature on the rat

---

35. See Appendix A, Table 1 for a summary chart of the studies that
     have been discussed.

and Flynn, Venegas, Foote and Edwards (1970) or Flynn (1967) for a

review of the work that has been done with the cat. Last, no mention

was made of the effect drugs have on the predatory response. This

area has mushroomed within the last ten years; apparently researchers

have grown wise to the fact that like the barpress the killing res-

ponse, once established, is also highly stereotyped and constant,

hence quite suitable for drug analysis. The effect stimulants,

depressants, anti-depressants, tranquillizers, psychotropic drugs,

etc. have on the rat's predatory response is now well documented and

examples can be found in Garnitti and Sigg (1969), Clark (1962a),

Horovitz, Piala, High, Burke and Leaf (1966), Kilby, Moore and Harris

(1973), Kilby, Moore and Hall (1973), Panksepp (1973c), Valzelli (1967),

Vogel and Haubrich (1973).

From time to time in the preceding review moot and ambiguous

points have been indicated which needed further clarification. The

effect hormones have on the predatory response is a good example.

Very little work has been done in this area and that which does

exist is of a conflicting nature. What effect experience has on

the development of the predatory behaviour still offers many possib-

ilities for future research. For example, Leyhausen's and Ewer's

notion that a cat passes through a critical period during which its

predatory behaviour is most likely to develop is an interesting point

but it needs empirical verification. The effects certain kinds of

infantile stimulation, such as handling, exposure to cold, electric

shock, etc. is another area of research which has been surprisingly

neglected. Further, no one to this author's knowledge has attempted

to correlate the incidence of prey killing (in the rat) with other

commonly studied laboratory behaviours such as open field ambulation, maternal and exploratory behaviour.

Above all, more research is badly needed with predators other than the albino rat. The eminent Frank Beach (1950) issued this plea a quarter of a century ago in his classic paper The Snark was a Boojum. Apparently, though, comparative psychologists who conduct research on the topic of predatory behaviour continue to remain oblivious to the existence of species other than the albino rat. As noted earlier most of the laboratory investigations concerned with mammalian predatory behaviour have been conducted with this species. The reluctance of the laboratory investigator to abandon the rat probably stems from the fact that rats are readily available and easily maintained but more importantly their widespread use probably stems from the fact that their predatory response can be easily elicited (nearly 100% will kill frogs). However, researchers must face up to the realization that if their knowledge of mammalian predatory behaviour is to substantially advance then they must start working with a variety of species. Future research on the predatory behaviour of laboratory mammals should be undertaken with this goal in mind.

Fortunately, some steps in this direction have already been taken. For instance, Thomas' research on the predatory behaviour of domestic mice seems promising (Thomas, 1969, 1971, 1972), and the well-known rodent psychologist Robert Boice reports that one of his students has recently initiated a programme of research on the predatory behaviour of the grasshopper mouse (R. Boice, personal communication, 1971).

Thus credit must be given to those researchers who have
attempted to broaden the range of species under study. Neverthe-
less, there is one commonly studied laboratory rodent that has been
totally neglected and that is, needless to say, the golden hamster.
One would initially think that with the great increase in the number
of researchers studying rodent behaviour someone, surely, would have
addressed himself to the problem of predatory behaviour in this
species. However, to this date, not a single publication on hamster
predatory behaviour has appeared in any English speaking scientific
journal.[36] Thus, broadly speaking, the experiments to be reported
in this treatise can be viewed as an attempt to remedy this deficiency.

Before we concern ourselves with the experiments we shall
attend in the first instance to the golden hamster. Since we will
be examining this species' predatory behaviour it would be best to
uncover, initially, exactly what we know about the golden hamster
in terms of its feeding habits, food preferences and related
behaviours. Hence, this topic along with a description of the
initial pilot study this author undertook will be the focal points
of discussion in Chapter 3.

---

36. The only paper on this topic which this author could find
     appeared in a German journal in 1968 and it will be dis-
     cussed in detail in the next chapter.

3

THE GOLDEN HAMSTER: NATURAL HISTORY, CLASSIFICATION

AND BEHAVIOUR

3.1. NATURAL HISTORY AND CLASSIFICATION

The species, <u>Mesocricetus auratus auratus</u>, was first discovered

in 1839 by a zoologist named G. R. Waterhouse who found a lone specimen

in northern Syria (Waterhouse, 1839). Waterhouse, no doubt, was

probably impressed with this animal's intensive hoarding behaviour

along with its striking golden colour; hence, the common name event-

ually coined for this new found species was 'golden hamster' (the

German translation of hamster is to hoard or store). Another specimen

was again found in the same area in the early 1900's (Burton, 1962)

but on the whole the scientific world remained oblivious to these

discoveries until 1930 when another zoologist by the name of

B. Aharoni upturned a litter of eight while on an expedition near

Aleppo, Syria (Adler, 1948).[1] Of the eight captured four escaped

and one female was killed by a male; thus from the original litter

of eight, two females and one male remained. Aharoni presented these

three animals to the Parasitology Department of Hebrew University in

1. Whether or not the exact number was eight seems to be a bit con-
   troversial. Zim (1950), Burton (1962), Walker (1968), Morris
   (1965) and Harrison-Matthews (1971) all report that Aharoni
   originally found a litter of 12 with their mother.

July 1930 (he found his animals in May of that year). Shortly after

they were bred and distributed throughout the world. The Medical

Research Council here in England received their first shipment in

1931 and France received their shipment shortly after. The Public

Health Service in America received their first animals in 1938 and

until recently it was believed that all the golden hamsters in

captivity were descendants of these three littermates.[2] If this is

true then the present day laboratory hamster is a highly inbred

species.

M.a.auratus belongs to the order Rodentia, to the superfamily

Muroidea, to the family Cricetidae and to the genus Mesocricetus.

The wild species in the genus Mesocricetus can be found in arid

places from south-west Europe to Asia minor. However, the only

place the laboratory variety, M.a.auratus, has ever been found is

in and around the area of Aleppo. Murphy (1971) reports that they

appeared to be fairly plentiful in the cultivated fields of the

Syrian farmers.

Related species within the genus Mesocricetus include M.a.newtoni

(the Roman hamster), M.a. brandti (the Turkish hamster) and M.a.raddi.

Genetical research has shown that differentiation of species within

this genus can be made on the basis of chromosome number; for example,

M.a.brandti possesses two fewer chromosomes than M.a. auratus (Wharman,

1959, reported in Whitney, 1963). The most common subspecies of the

---

2. Murphy (personal communication, 1972) reports that he has recently
   captured 12 wild hamsters of the golden type while on a reconnais-
   ance expedition near Aleppo. According to Murphy these animals
   are now breeding in his laboratory in the U.S.A.

family Cricetidae include <u>Cricetus cricetus</u> (commonly known as the

European hamster or black hamster) and <u>Cricetulus barabensis</u> (common-

ly known as the Chinese hamster or grey hamster). In the wild the

black hamster ranges between the western coast of Europe and northern

India and the grey hamster can be found between the east coast of

China and the eastern shores of the Caspian sea (Whitney, 1963).

Because of the geographical overlap between the black and grey

species, the golden species, which is intermediate in size, may be

a hybrid arising from their crosses (Sachs, 1952).

3.2.   BEHAVIOUR OF THE GOLDEN HAMSTER

Unfortunately, very little is known about the natural habits

of the golden species.[3] Apparently, the extent of our knowledge is

that they are nocturnal in habit, live alone in burrows and that

as adults are extremely pugnacious (Walker, 1968). To this date

no one to this author's knowledge has made any observations on this

species in the wild.[4] All of what we know about the hamster behaviour

comes from the laboratory investigations. No attempt at an exhaustive

review of the behavioural literature on this species will be made for,

at best, most of it is only indirectly concerned with the subject

matter at hand. As a passing note, though, it is of interest to

know that the first behavioural study on the hamster appeared in

---

3.   From this point on in the text when reference is made to
      golden hamster, golden species, or just simply hamster it
      should be taken to mean the laboratory type; i.e. <u>M.a.auratus</u>.

4.   However, Murphy (1971) is now studying the behaviour of the
      hamsters he caught in the fields of Aleppo in his laboratory.
      He reports that he has observed no gross morphological or
      behavioural differences between the domestic and wild types.

1946 (Reed and Reed, 1946) and subsequent to that the bulk of the

research has been concerned with: 1) agonistic behaviour (Brain, 1972;

Grant, Mackintosh and Lerwill, 1970; Lerwill, 1968; Lerwill and

Makings, 1971; Payne, 1973; Payne and Swanson, 1970); 2) maternal

behaviour (see Moltz, 1971 or Richards, 1967 for a general review

and see Noirot, 1972 for a review of the effects of priming);

3) territorial behaviour (see Murphy, 1970); 4) open field behaviour

(Swanson, 1966, 1967, 1969 or Tobach and Gold, 1962); 5) sexual

behaviour (Beach and Rabedeau, 1959; Carter and Schein, 1971;

Eckmann and Carter, 1971; Johnston, 1972, 1974; Krehbiel, 1952;

Miller, 1972; Noble, 1973a, 1973b); 6) hoarding behaviour (Hammer,

1972; Scelfo and Hammer, 1969; Smith and Ross, 1950, 1953; Waddell,

1951); 7) social dominance (Drickamer, Vandenberg and Colby, 1973;

Drickamer and Vandenberg, 1973; Lawlor, 1963) and 8) circadian

rhythmicity (Ashoff, Figala and Poppel, 1973). Recently, there has

been a spate of interest in the effect hormones have on the develop-

ment of agonistic and sexual behaviour (Doty, Cater and Clemens,

1972; Johnson and Tiefer, 1972; Nucci and Beach, 1971; Payne and

Swanson, 1972a, 1972b, 1972c; Swanson and Crossley, 1971; Tiefer,

1970; Tiefer and Johnson, 1971) and the effects of centrally and

peripherally induced anosmia (Carter, 1972; Devor and Murphy, 1972,

1973; Leonard, 1972; Lisk, Zeiss and Ciacclo, 1972; Murphy and

Schneider, 1970; Powers and Winans, 1973).

Although information on hamster behaviour continues to accumu-

late at an unprecendented rate, information on its predatory behaviour

and associated food habits is still badly needed. What we do know is

that hamsters in the wild feed largely on wheat which they hoard in their underground burrows (Murphy, 1971). Moreover, and of utmost importance, Murphy has informed this author that there are numerous insects (particularly beetles) in the niche of the hamster upon which they also feed (Murphy, personal communication, 1972). Thus, in all likelihood, if what Murphy says is true, then hamsters in the wild are predatory. The well known rodent zoologist, H. Mendelssohn (of Tel-Aviv University), has also confirmed the fact that laboratory hamsters are very keen on insects and that in feral conditions they probably feed on insects to a certain extent (Mendelssohn, personal communication, 1972). Further, Landry (1970) in his comprehensive review of rodent feeding habits has ammassed evidence which shows that nearly all species in the order Rodentia feed on a wide variety of insects in the wild.

However, the only report to date which substantiates the belief that hamsters do in fact take insects was reported by a botanist named Jacobs quite some time ago (Jacobs, 1945). According to Jacobs his pet hamster escaped from its cage one weekend and when captured several days later he removed from its cheek pouches 13 sow bugs, 7 ants, 4 cockroaches, 2 flies and 1 hornet. He then went on to conduct an experiment and found that his subjects would choose insects voluntarily, even when other food was present. Jacobs further claims that some of his hamsters "hunted them out and pounced on them" (p-199).

Another study was published in 1966 which showed that hamsters

would attack, kill and eat other small mammals. However, the mammals in this study (Noirot and Richards, 1966) happened to be pups of their own species. The phenomenon under investigation was the effect prior exposure to hamster pups had on later maternal responsiveness. Briefly, the procedure consisted of presenting a pup (either 1, 5 or 9 days old) to a naive non-lactating female for a brief period and then subsequently testing her (for maternal behaviour) with a 5 day old pup. The point of concern for us in this study was the reaction a hamster showed when presented with the initial test pup. Noirot and Richards found that presentation of the one day old pup elicited attack and killing in all instances. Further, feeding on the pups always followed. These authors therefore speculated that attack behaviour towards pups "closely resembles reaction to the living prey" (p-8).

Aside from this study and the observations of Jacobs, the only other investigation directly concerned with the hamster's killing behaviour was conducted by a German named Hemmer (Hemmer, 1968). In his study Hemmer was chiefly concerned with the predatory behaviour of the related black hamster (Cricetus cricetus) but he did make some observations on the golden species. For prey, Hemmer offered his golden hamsters domestic mice and observed that the initial attempts to capture and kill were made by grasping and biting predominantly at the hind part of the prey's body; no orientation to bite at the neck was present. Often, in the initial attempts, a mouse escaped from a hamster's grasp and, in fact, at times even bit a hamster back. Eventually killing was accomplished by a series of repeated unoriented bites to the body. Hemmer also found that his subjects would usually

begin to eat dead prey from the head downwards; however, if offered

a mouse which was purposely cut open before hand so as to expose the

flesh, they would then commence eating from this spot rather than the

head. He thus concluded that a hamster was 'enticed' to start eating

from the exposed spot due to olfactory characteristics of the prey's

blood. Further, Hemmer systematized hamster predation into the follow-

ing five components: 1) appetitive behaviour; 2) pursuit; 3) catching

and killing; 4) throwing himself down on one side[5] and 5) cutting

and eating. Basically then, these are the major findings of the study,

which was largely observational in nature.

3.3. PILOT OBSERVATIONS

Thus, from the discussion in the previous chapter and from

what has been said so far in this one it is apparent that much needs

to be discovered about predatory behaviour in the golden hamster.

For these reasons this author commenced with a pilot study in order

to gather information on the following two points: first, would the

behaviour occur in the captive laboratory hamster and, if so, under

what conditions and with what methods would the behaviour be most

amenable to investigation? Second, it was asked, what prey species

would be most suitable for the hamster?

---

5.   It is not clear what Hemmer means by "throwing himself down
     on one side". This author takes it to mean that the hamster
     falls over on one side during the struggle with the prey.
     In his paper Hemmer includes a photograph which indicates
     that this is the case.

Concerning the latter, it was decided that the initial attempts

would be made with the insect species, _Locusta migratoria_, commonly

known as the African migratory locust. This decision was not made

arbitrarily; rather, it was made with the realization that hamsters

probably do feed upon insects in the wild and even possibly upon

locusts, for it is known that locusts are indigenous to the area

around Aleppo. Purchit (1967) who studied another rodent species,

the Indian desert gerbil, in an area not far from Aleppo noted,

"during the dry month _Meriones_ begins to feed upon insects and

particularly upon locusts which are abundant during that season" (p-31).

The procedures adopted for the pilot study consisted simply of

introducing a locust nymph into the home cage of a naive hamster

which was housed singly. Introductions continued for several suc-

cessive days and on each session a hamster was allowed ten minutes

to make capture. If it failed to capture within the allowed time the

locust was removed by the Experimenter. In total, observations were

made on 20 hamsters each approximately sixty days of age. During all

sessions qualitative notes were taken when needed.

The behaviour of a naive hamster when it first encountered the

prey was usually characterized by ambivalence. Bouts of approach,

exploration, withdrawal, followed by additional bouts of approach,

exploration, withdrawal typically occurred during the first few

minutes of the interaction. The initial explorations were usually

made at a distance of about one to two inches (from the prey) and

usually lasted about three to four seconds. Further, they were often

followed by intense withdrawal; that is to say, a hamster would

explore, abruptly turn and flee and then begin a vigorous bout of scrabbling (scrabbling being defined as a behaviour in which a hamster claws at the wall, often hopping up and down, and moving along the wall as if trying to climb out; see Shettleworth, 1973). Subsequent explorations tended to decrease in frequency as well as duration. However, when a hamster did explore it seemed to spend more time exploring the anterior end (of the locust). Eventually withdrawals following explorations dropped out and were replaced by nips at the locust. Surprisingly, however, a hamster often withdrew abruptly following its first few nips, so the initial sequence of approach, exploration, withdrawal was now replaced by approach, exploration, nip, withdrawal. The initial nips also differed from subsequent nips. The first few lacked orientation and left the locust uninjured, whereas later nips were directed towards the anterior end and usually left the locust severely maimed. After about the second or third ten minute presentation, withdrawals following nips dropped out and instead the hamster attempted to capture the locust by initially seizing it with its mouth and then immediately grasping with the forepaws. However, the initial attempts at capture were often unsuccessful, for after being grasped, the hamster either dropped the locust or the locust forcibly jumped out of the hamster's paws. Subsequent attempts were more successful and after getting a firm hold on the locust a hamster on most occasions began to eat it, usually from the anterior down. Following eating, a hamster often began a vigorous bout of face washing.

On the other hand, a hamster, on occasion, before eating would run around the cage with the locust in its mouth, obviously in a very
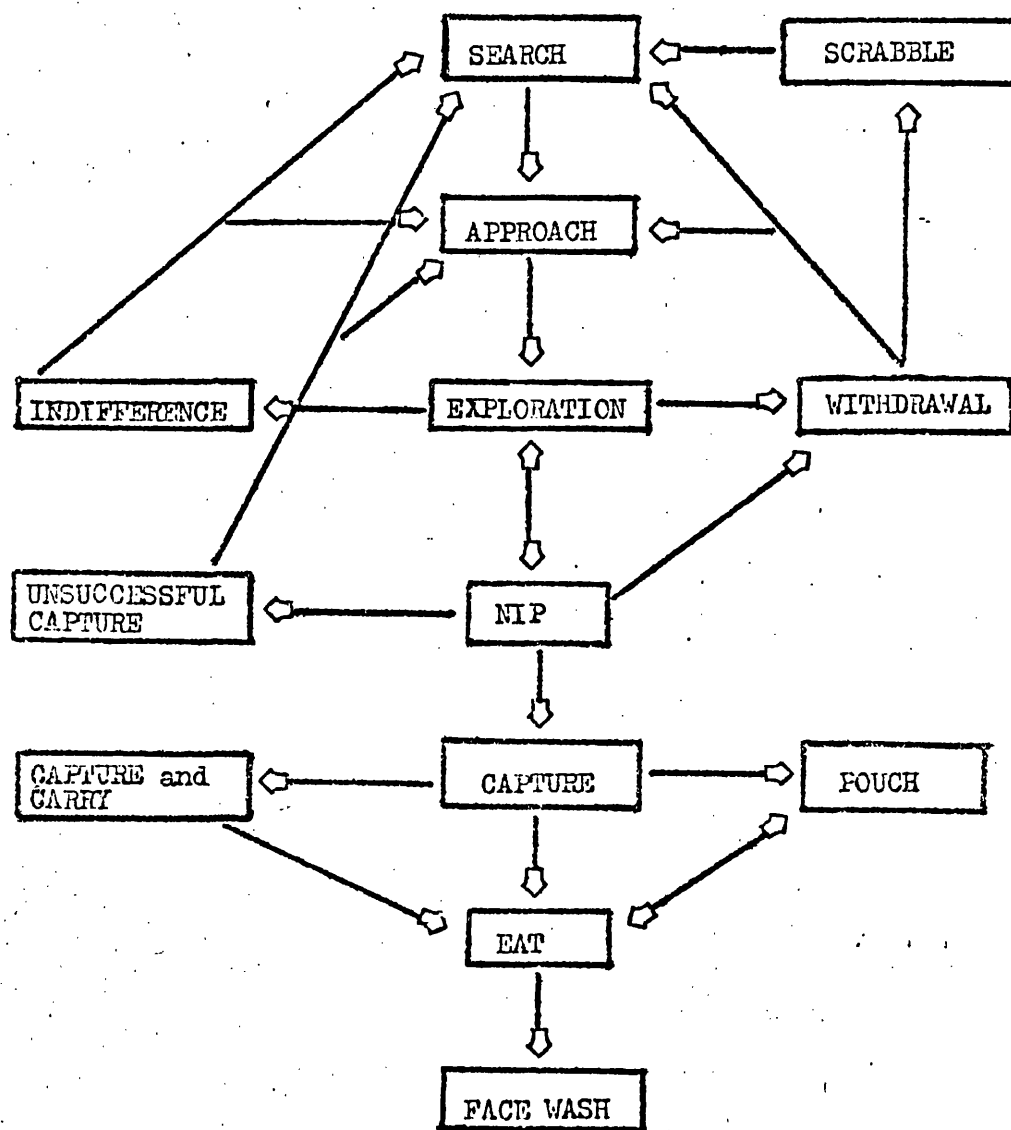
Figure 3.1. Ethogram of the sequences of behaviour exhibited by a hamster when confronted with a locust. The sequence for those subjects who capture is usually ended by eat followed by face wash, or pouch. See text for further explanation.

excited state, and when this occurred it was referred to as

'capture and carry'. On other occasions a hamster would very

quickly pouch the prey; that is to say, it would capture the

locust in the normal manner and then immediately shove it into

one of its cheek pouches. When this author first witnessed the

act of pouching he was dumbfounded with the lightning speed with

which it occurred; however, it seemed that a hamster had to have

the experience of several successful captures before it could

become this efficient. How long a hamster kept the locust in

its pouch, after pouching, varied; at times it was immediately

removed (followed by feeding) while at other times there was an

interval of ten to fifteen minutes.

An ethogram of the sequences of behaviour which lead to capture

and consumption are represented diagrammatically in Figure 3.1.

Most of the behaviours and the sequence in which they occur have

been described in the preceding paragraph; however, additional

explanation is needed. First, in order to clear up any ambiguity

that still may exist it would be best to operationally define each

of the behaviours that are represented. Searching behaviour consists

of forward unoriented locomotor movement with the head held low to

the ground and moving rapidly from side to side. Further, this

pattern is usually accompanied by rapid and continuous vibrissae

movement. Approach behaviour may be defined as locomotor movement in

the direction of the prey. Exploration (of the prey) occurs whenever

a hamster faces the prey at a distance of less than three inches while

simultaneously moving its vibrissae up and down. Withdrawals occur

whenever a hamster moves abruptly (usually in the opposite direction)

from the locust following an exploratory bout. Indifferent behaviour

may be regarded as any behaviour not directly associated with the

capture; thus, behaviours like burrowing, defecation and territor-

ial marking should be regarded as behaviours of the indifferent type.

Capture, capture and carry, scrabble and pouch have already been

described in the preceding paragraph. Lastly, face wash should be

self-explanatory. Second, the behavioural sequence as indicated in

Figure 3.1 usually does not begin with the search component, but

instead begins with approach. On most occasions after the locust was

introduced the hamster located it from a distance (possibly through

vision) and made a direct approach without search. Search only

occurred if a hamster lost cognizance of the location of the prey

during an encounter. Thus, following withdrawal, unsuccessful cap-

ture, or an act of indifference, a hamster would then either directly

approach the locust, or alternatively, if it was unable to locate the

locust at a distance, search for it and then approach. Therefore, in

Figure 3.1 arrows are drawn from the withdrawal, unsuccessful capture

and indifferent components to both the search and approach components.

However, it may again be emphasized that in most instances a hamster

made a direct approach to the prey; search rarely occurred.

Third, the reader should note the bidirectional arrows between

the nip and exploration components. This bidirectional arrow accounts

for the fact that if a hamster did not withdraw, or attempt to capture

following nip, then it usually made another exploration followed by

Figure 3.2. A hamster eating a locust which it had just captured. The photograph exemplifies the typical feeding posture in the experienced captor; i.e. squatting on the hindlegs with both forepaws grasping the prey around the thorax so that the anterior end points up towards the mouth. Eating then commences from the head down.

another nip. This sequence of explore - nip, explore - nip, continued until a hamster attempted capture or withdrew.

Fourth, after a hamster had experienced several successful capt-
ures then the sequence of approach, exploration, nip, capture and eat.
(or pouch) became a highly stereotyped sequence. The experienced
hamster captor usually directed most of its exploration towards the
anterior (of the locust) and its nips were almost always directed
towards this end. Capture was always accomplished by seizure with
the mouth immediately followed by grasp with the forepaws. Eating
in the experienced captor invariably commenced from the head down
and in most cases this was accomplished by squatting on the hindlegs
while holding the locust up off the ground with both forepaws.
Figure 3.2 illustrates these points clearly, for it shows an exper-
ienced captor eating a locust which it had just previously captured.

Fifth, it should be realized that the behaviours listed in
Figure 3.2 account for all possible behaviours that a hamster could
exhibit when confronted with they prey. Those hamsters which did
not capture (not all captured in this pilot study) usually behaved
with withdrawal or indifference following exploration. In very few
cases did they nip and rarely did they ever attempt capture.

Last, it should be noted that the word 'kill' is never used.
The abandonment of the word kill for that of capture is desirable
for two reasons. First, the behaviours concerned with seizure with
the mouth and grasp with the forepaws are best described by the word
capture. Second, and most important, a hamster probably never did

kill a locust. If kill is defined as the cessation of all bodily

movements, as it is when a rat kills a mouse, then surely it does not.

Once captured, and even after being bitten several times, the legs of

the prey often continued to twitch. Thus, for these reasons, a

hamster never did kill - it only captured.

Some comments should also be made about the behaviour of the

prey. In all cases during these pilot observations only active

locusts were used; thus, when introduced into a hamster's cage a

locust usually hopped about quite frequently. During a bout of

exploration on part of the hamster a locust often remained stationary;

however, it was not uncommon for it to hop. Whether or not it hopped

seemed to depend on the orientation of the hamster; for example, if

it approached and then explored the prey head on then this usually

caused the locust to hop. However, if a hamster approached from the

side or from behind and likewise continued to explore from this dir-

ection, then in most instances the locust remained stationary. Seldom,

however, did the locust ever remain stationary for more than 15 to 20

seconds. If a locust happened to hop while a naive hamster was in

the midst of an exploratory bout, then this usually elicited immediate

withdrawal on part of the hamster. Further, for the purposes of

classification, the locust appeared to be prey of the innocuous type

(see Ewer, 1969). On no occasion did it ever show any signs of def-

ence (other than hopping away) and in all cases the hamster easily

overpowered it with several successive nips to the anterior end.

In summary, the observations from the pilot study strongly sug-

gested that with experience a hamster became a more skillful and

efficient locust captor. It was observed that when initially con-
fronted with the locust a hamster behaved with abivalence, but with
experience it came to capture in a highly reliable and stereotyped
manner. Hence, these qualitative observations have set the stage for
formal experimentation and so it is the experiments to which we will
now turn our attention.

SECTION II

EXPERIMENTAL STUDIES

4

SUBJECTS, APPARATUS AND METHODOLOGY

The aim of this chapter will be to present a general account
of the subjects, apparatus and methodological features common to
all of the experiments to be subsequently reported. This step
should prevent redundancy from occurring in the text. Subjects,
experimental design, methodology and any anomalies which are spec-
ific to any one experiment will be appropriately discussed when
the experiment itself is formally dealt with.

4.1.   SUBJECTS

4.1a.   The Predators

Nearly all of the hamsters used in the experiments were
descendants of six male and six females purchased from a commercial
dealer (The Coombehurst Breeding Establishment, Basingstoke, Hamp-
shire) in the winter of 1971. All were golden type as previously
described (see Chapter 3) and all were derived from a genetically
heterogeneous stock. Breeding the adults in order to obtain naive
young for experimental purposes was accomplished according to the
methods outlined in Whitney (1963). Basically, this consisted of

test breeding or pen breeding. In the case of the former the female was removed from her own individual maternity cage and placed in a cage containing several males. If sexually receptive the female assumed the typical lordosis posture and copulation with the males followed. After about 30 minutes the female was removed and returned to her own maternity cage. Subsequent to mating she was checked routinely (every two or three days) for physical signs of pregnancy, and between the 13th and 16th day (a hamster's gestation period, on average, is just under 16 days) she was checked daily with minimum disturbance for signs of having littered. Following birth, and until weaning, the mother and pups were left entirely undisturbed except for having to refill the food tray and water bottle when needed or upon the insertion of greens, carrots and milk into the cage.

The procedures employed in pen breeding the animals were essentially the same, with the exception of the way in which pregnancy was induced. Pen breeding was accomplished by communally housing three to four females with three to four males, each approximately 75 days of age, in an adequate size cage. Females, as above, were checked routinely for physical signs of pregnancy and when pregnancy was detected she was removed and re-housed individually in a maternity cage. During pen breeding attempts were made to detect pregnancy as early as possible and in almost all cases pregnancy was detected by the ninth or tenth day of gestation. Very few cases of 'pseudo' pregnancy occurred. Further, pregnant females with an unusually high number of wounds (from fighting) were ignored.

'In order to keep the breeding programme viable it became necessary to select subjects from already completed experiments. In most instances the females chosen were virgin, hence nulliparous. On some occasions, though, a female after her initial litter was weaned was again recycled into the breeding programme; hence females were multiparous. In addition, efforts were made to keep breeding between males and females as random as possible so as to ensure a genetically heterogeneous stock for experimental purposes.

As indicated, females were housed pre-partum and post-partum in their own individual maternity cage. All maternity cages were adjacently shelved on a communal breeding rack which could hold, maximally, 20 such cages. The cages, which measured $17\frac{1}{2}$ x 11 x 8 in, consisted of a polypropylene bottom with a removable galvanized steel top (type RB 3 manufactured by the North East Kent Plastic Cages Ltd., Dartford, Kent). Bedding in each cage consisted of wood chips and in no instance was it ever changed following parturition, regardless of how soiled it might have become. Nesting material in the form of tissue or shredded newspaper was adequately provided.

Following parturition mothers and their young were maintained on ad lib water and laboratory chow. The brand of chow used was Breeding Diet for Rats and Mice (manufactured by Berbert C. Styles Ltd., London). Powdered milk, dissolved in tap water, was available throughout most of the lactation period. In addition, fresh greens (cabbage leaves, brussel sprouts and lettuce) and carrots were regularly provided.

In all of the experiments subjects were weaned between 19 and 25 days of age. In most of the experiments, however, weaning took place between 23 and 25 days. This two day range was employed mainly to cut down on the work at weekends. The procedures during weaning consisted of, initially, removing the mother from her cage and then subsequently removing each pup, individually, so that it could then be weighed, sexed and assigned to a treatment group. Handling the pups was kept to a minimum; never were they handled prior to weaning and the only time they were handled during weaning was when they were transferred from the maternity cage to the weighing scale and from the weighing scale to the experimental compartment. Sexing was readily accomplished by a brief examination of the genital organs.

The room in which all the animals were bred and in which all testing took place was located in the basement of the Department of Psychology. The room measured approximately 45 x 12 x 12 ft and was constructed of brick walls with a cement floor and ceiling. No windows were present. Sound in the room was absorbed especially well and the everyday noise which penetrated into it from the outside corridor was minimal. Artificial light, automatically controlled by electric timers, was provided in cyclic phases of red and white. Phase one, which lasted from approximately 9:00 hours to 18:00 hours, consisted of moderately bright (approximately 6 lumens/sq. ft.) red light. In total, twelve red bulbs, forty watts each in power, were distributed as evenly as possible throughout the room. In phase two, moderately bright white light (approximately 8 lumens/sq. ft.) was provided from approximately 18:00 hours to 9:00 hours. Care was

taken to ensure that in both the red and white phases illumination

into each individual compartment was roughly equal, regardless of

its position in the experimental room. Ventilation in the room was

adequate and the room temperature ranged from 68° - 75° F; relative

humidity was approximately 40%.

4.1b.   The Prey

The locust culture was also established in the winter of 1971.

The initial stock of Locusta was generously supplied by the Anti-

Locust Research Centre in London. All locusts were kept in a small

room on the top floor of the Department of Psychology. Details of

the cages in which they were housed, the methods of breeding, feed-

ing routine, maintenance procedures, etc. can be found in Hunter-

Jones (1961) or Ashby (1967).

Generally, all locusts which served as prey were raised in

perspex-fronted sheet-metal cages each approximately sixty litres

in capacity. Nymphs were kept separate from adults. All were fed

daily on fresh grass supplemented with hay and bran. Water was also

provided. The temperature in each cage was maintained at approximately

87°F $\pm$ 3°. On testing days the prey was transferred from its room

upstairs to the hamster room downstairs in a plastic bottle. Inactive

prey, prey whose exoskeleton was soft due to having recently moulted

and prey with legs missing were never used for testing. At the end

of a day's testing prey which remained in the bottle were transferred

back into the cage from which they came. A photograph of Locusta in
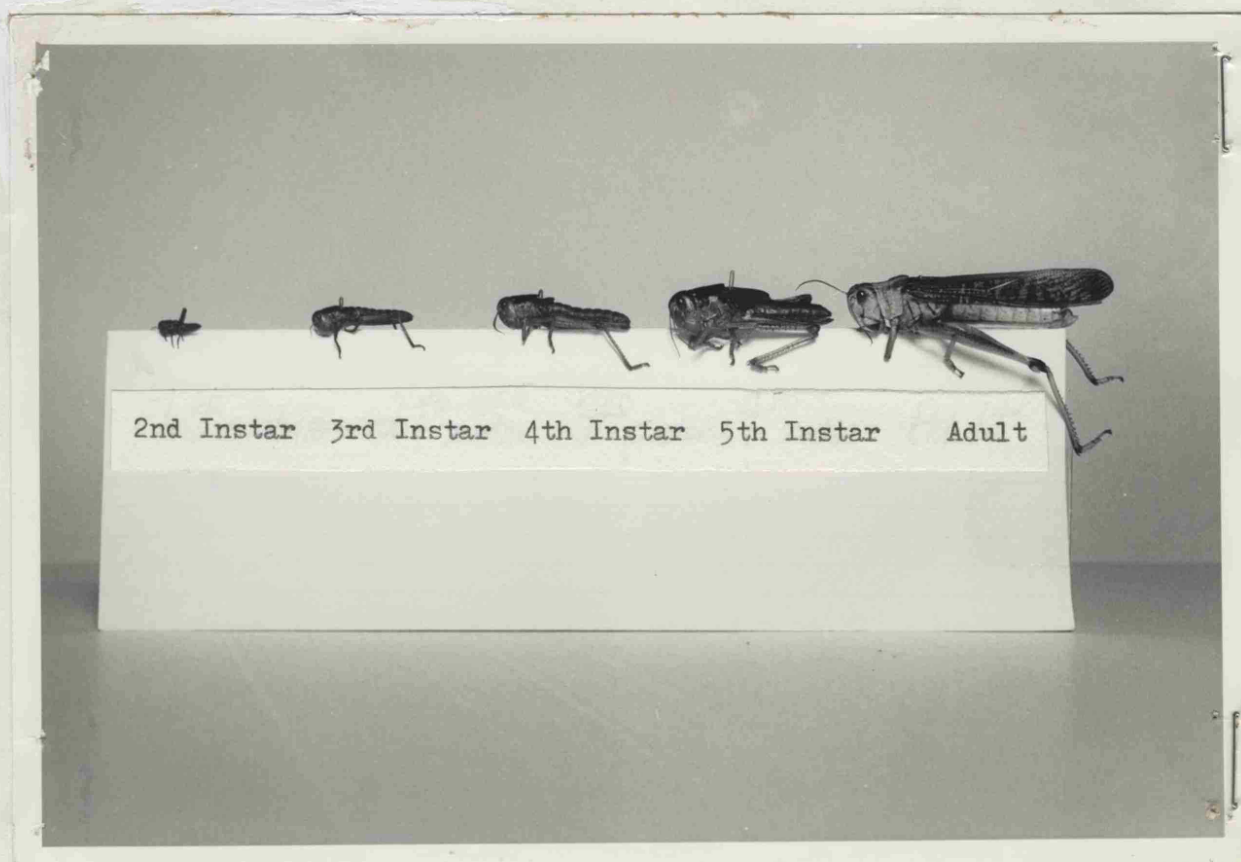
Figure 4.1. Photograph of the prey, _Locusta migratoria_, in various
stages of development. During development this species moults five
times (excluding the intermediate moult) and with each moult it
roughly doubles in size. The first instar (not pictured) is approx-
imately 1/8 in. long, the second 1/4 in., the third 3/8 in., the
fourth 1/2 in., the fifth 1 in., and the adult approximately $1\frac{1}{2}$ - 2 in.
long. In most of the experiments to be reported nymphs of the 4th
instar were used.
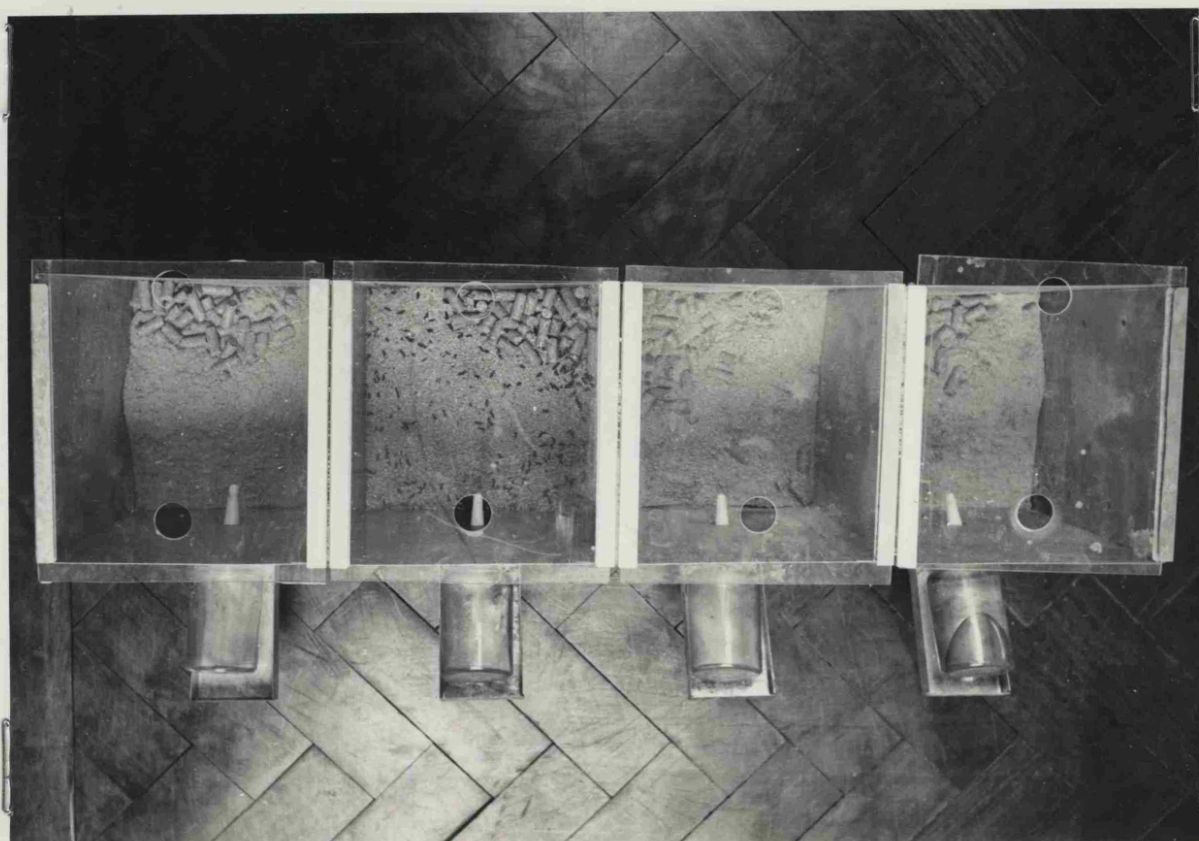
Figure 4.2. Photograph of the testing compartments. In
this photo a set of four is shown. See Figure 4.3 for a
photo of a set of eight and see text for specifications of
their design.
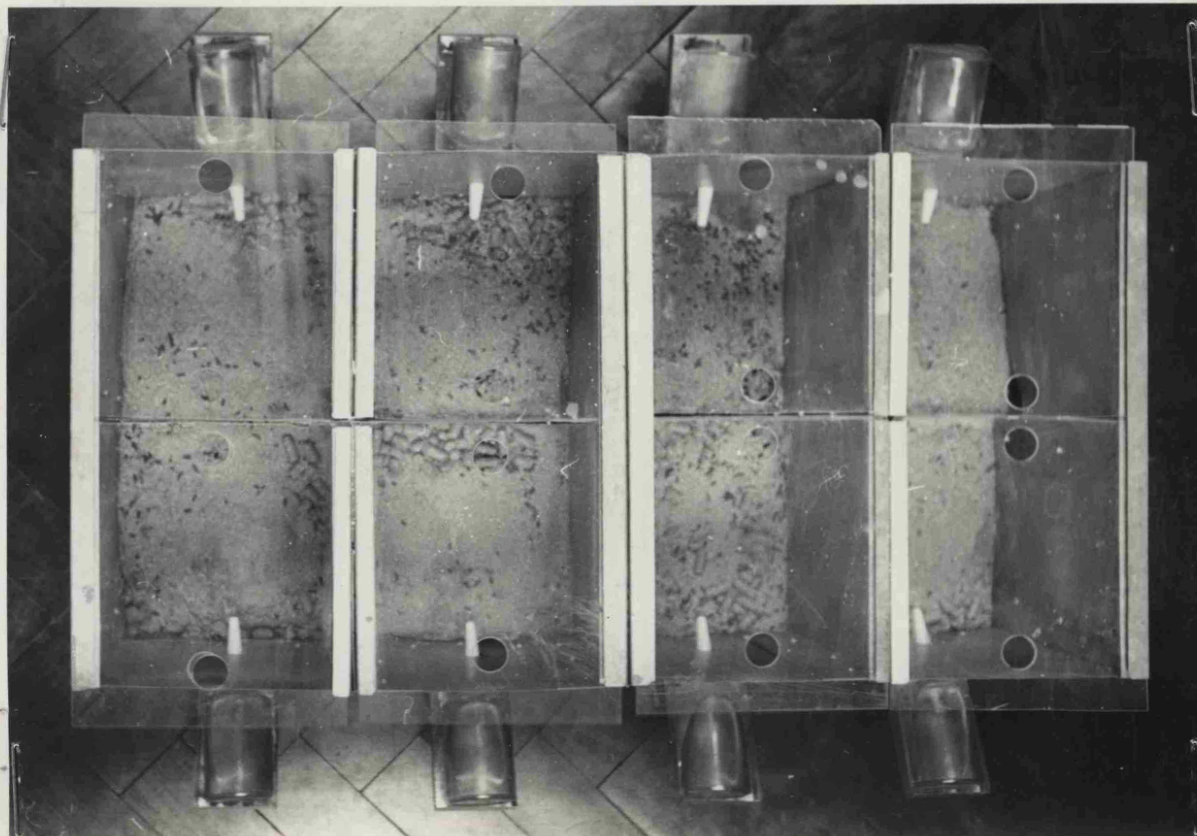
Figure 4.3. Photograph of the testing compartments. In this photo a set of eight is shown. See Figure 4.2 for a photo of a set of four and see text for specifications of their design.

Figure 4.4. Photograph of the experimental room looking from the front to the rear.

Figure 4.5.   Photograph of the experimental room looking from
the rear to the front.

each stage of development appears in Figure 4.1. In most of the experiments only prey of the 4th instar were used.

4.2.   APPARATUS

Singly, the most important piece of apparatus was that of the specially constructed testing compartments. A photograph of the compartments appears in Figure 4.2 and 4.3. As shown, they were joined in groups of four or eight and each individual compartment measured 7 x 7 x 9 in. All were constructed of galvanized sheet metal and all were fitted with a sliding perspex top. In addition, all tops contained one $\frac{3}{4}$ in. hole located at each end. One large sheet metal tray, measured to size, served as a common floor for all the joined compartments. The floor could easily be removed for cleaning purposes by lifting the group of joined compartments up from it and dumping the soiled bedding into a wastebin. On the outside front of each compartment a water bottle tray was attached, the position of which allowed the nozzle of a resting water bottle to pass through a small hole in the compartment front. For the bedding a $\frac{1}{4}$ in. layer of sawdust was provided in each compartment.

When in the testing compartments subjects were both visually and tactally isolated from all other hamsters. However, subjects in adjacent compartments could hear and smell each other.

The arrangement of the testing compartments in the experimental room is shown in Figure 4.4 (front view) and Figure 4.5 (rear view).

155.

As shown three groups of eight compartments were located in the

centre of the room on a large size table. One group of four compart-

ments was positioned on top of the breeding rack and the rest (13

sets of four compartments) were located on shelves attached to the

side walls. In total, 80 compartments were available for testing

purposes. Further examination of Figure 4.4 and Figure 4.5 shows

the position of the breeding rack, breeding cages, holding cages

and the arrangement of the red and white bulbs.

Aside from the testing compartments the other main piece

of apparatus was a two speed, twelve-channel, multiple pen recorder

(manufactured by Everett Edgcumbe, London). When it was used, though,

only five channels were needed and the drum holding the recording

paper was set to move at a constant .793 cm/sec. The pens were

activated manually through the depression of buttons on a separate

keyboard.

Additional apparatus included a stopwatch which was employed

in every experiment to time the length of a test session and, when

needed, to record latencies to capture.

4.3.   GENERAL PROCEDURES

Subjects when weaned were placed individually in a freshly

cleaned testing compartment (i.e. the walls were wiped with a damp

rag and a new layer of sawdust was inserted). In all of the experi-

ments <u>ad lib</u> access to lab chow and water was permitted post-weaning

and occasionally carrots were provided. Further, in most cases the

bedding in a compartment was left unchanged for the duration of an

experiment. When a change was required it was usually for sanitary

reasons and in no instance was one ever made immediately preceding

a test; an interval of several days always intervened. During a

change a subject was gently lifted out of a compartment in a coffee

mug and temporarily placed in a small holding cage. A fresh layer

of sawdust was then inserted and the subject was returned.

Other precautions were also taken to minimize the disturbance

of subjects when in the testing compartments. Never were they

handled post-weaning and visitors into the experimental room were

kept to a minimum. Food, when needed, was always provided by gently

lowering it to the compartment bottom. Water bottles which needed

re-filling were always placed back within minutes after being removed.

All testing was conducted between one and six hours after the

onset of the red lights. At the beginning of a testing day (usually

around 11:00 hours) subjects that were to be tested were initially

checked to see if they were awake. Those who were sleeping (not

very many) had their compartment top rattled in order to awaken them.

If this failed the Experimenter gently tapped a subject on its back

with his finger. Further, if a subject happened to be involved in

some intensive consummatory behaviour, like burrowing in a corner

(bouts of burrowing occasionally lasted up to five minutes) or eating,

the compartment top was gently rattled. This step served to interrupt

the ongoing behaviour and usually caused a subject to rear and start

sniffing the air; testing then commenced four to five minutes later.

Tests were always started by introducing the prey into the compartment through one of the holes in the perspex top. The hole through which the prey was dropped depended on where the hamster was at the time; for all introductions the hole furthest from the hamster was chosen. Observations were then made by looking into the compartment through the perspex top. Never did the Experimenter peer directly into the compartment during a test; observations were always made at a distance (about a foot) to prevent visual detection of the Experimenter by the hamster. All tests were started the moment the prey was dropped into the compartment, and all ended upon the completion of a successful capture or capture and pouch. Tests were also terminated if the prey was removed by the Experimenter. If during a test the prey managed to climb up and cling to one of the compartment sides, so as to be out of reach of the hamster, it was quietly prodded back to the compartment floor with the end of a pencil.

The behaviours examined have already been described in the previous chapter. In most of the experiments they were capture, unsuccessful capture, exploration, withdrawal, nip, and unsuccessful capture. In the first experiment (Chapter 5) the amount of prey eaten and whether or not it was pouched or carried after capture was also noted. The principal measures to be reported were latency to capture and the frequency of prey exploration, withdrawal (from the prey), nip (at the prey) and unsuccessful capture. A successful capture was defined as an uninterrupted hold on the locust with the forepaws for at least 15 seconds and an unsuccessful capture was recorded
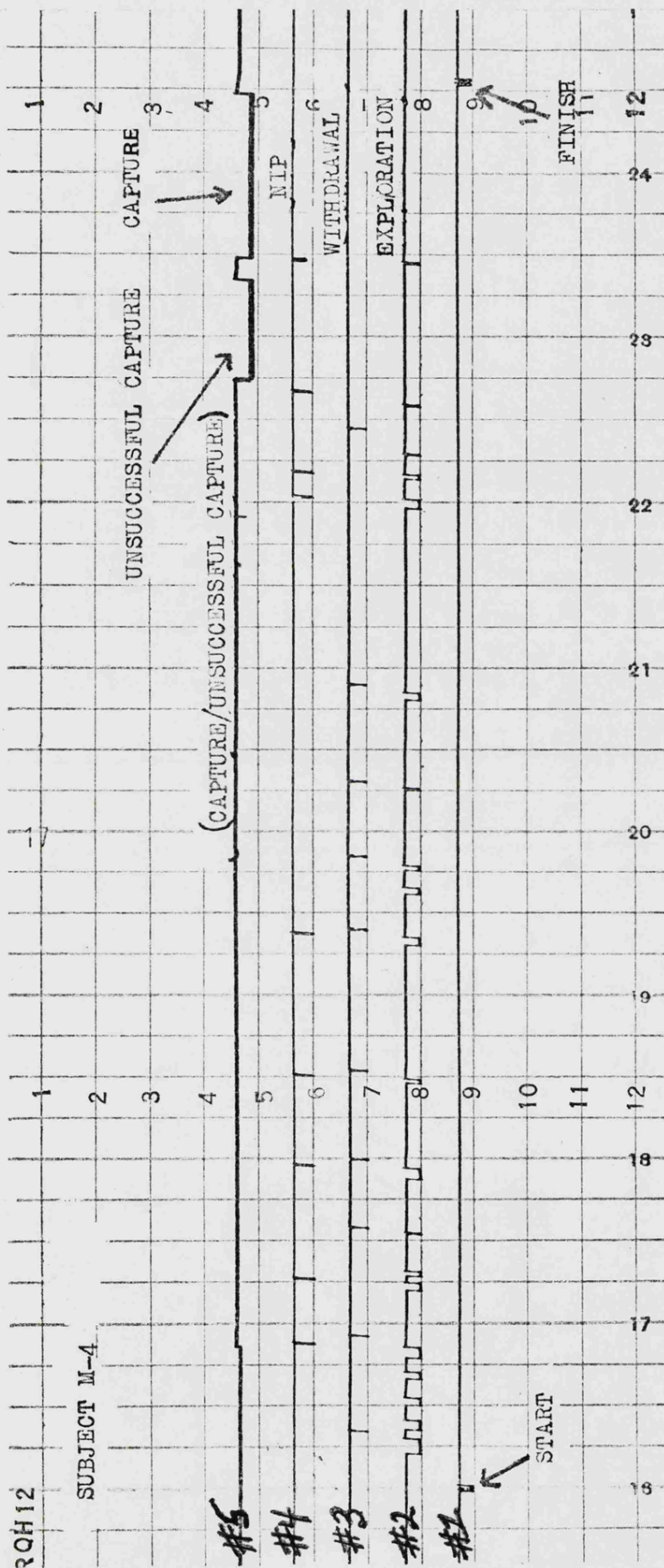
Figure 4.6. Sample of a recording taken on a multiple-pen recorder during a hamster – locust interaction. Blips on line 1 indicate the start and finish of a test session, and blips on lines 2 – 5 indicate the frequency and duration of exploration, withdrawal, nip, and unsuccessful capture. See text for additional details.

158.

if a subject grasped the prey but failed to hold it for this length

of time. Exploration occurred whenever a subject stood facing the

prey at a distance of two inches or less while simultaneously moving

its vibrassae up and down. Withdrawal was recorded whenever a subject

moved abruptly from the prey following an exploratory bout. Nip was

recorded whenever a subject attempted to bite the prey. All raw data

were analysed with the statistical tests presented in Klugh (1970),

Siegel (1956) and Winer (1970).

A sample of multiple-pen recording for a single session appears

in Figure 4.6. As shown, five channels were used with each line

representing a single channel. The first channel (line 1) was activ-

ated when the test session commenced and when it terminated. As

indicated, lines 2 - 5 represent, respectively, exploration, with-

drawal, nip and unsuccessful capture. In the example presented,

subject M4 made 20 explorations with an accumulated duration of

16.6 seconds, ten withdrawals, nine nips and one unsuccessful capture.

Latency to capture was 170 seconds. Latencies and durations were

derived by measuring the distance in centimeters between any two

blips (for example, the distance between the onset and termination

of an exploratory bout) and multiplying it by .793 (the speed at which

the paper moved in centimeters).

All in all, then, the procedures prior to and during a test,

the behaviours recorded, the method of recording and the apparatus

in which the testing took place were relatively simple and straight-

forward. In summary, what this consisted of was breeding the animals

in order to obtain naive subjects for experimental purposes. On

the day of weaning, which was usually between 23 and 25 days of

age, subjects were transferred from their maternity cages and re-

housed individually in 7 x 7 x 9 in. testing compartments. Tests

were then conducted by introducing the prey, a locust nymph, into

the compartment though the compartment top. Reactions of the

hamster were then recorded manually by the Experimenter on a

multiple-pen recorder. Variations from these general procedures

will be dealt with in detail in the text at the appropriate time.

5

THE INFLUENCE OF AGE AND EXPERIENCE

Observations from the pilot study (see Chapter 3) suggested

that a naive hamster's reaction to a locust changed with experience.

In most cases ambivalence characterized the initial phases of the

interaction but with repeated presentations of the prey the ambiv-

alence waned and capture ensued. The first experiment was thus

designed to quantify these qualitative observations. In addition,

the experiment was designed to ascertain what effect age had on the

predatory response.

5.1. DESIGN AND PROCEDURE

The subjects were 112 hamsters derived from eighteen litters

born between 2nd April and 3rd June, 1971. Following weaning, which

occurred between 23 and 25 days of age, subjects were randomly assigned

to four experimental groups. Testing commenced for the subjects in

each group when they reached 30, 40, 50 or 90 days of age. The

experimental groups were thus designated 30 Day Old, 40 Day Old,

50 Day Old and 90 Day Old. When a subject reached its respective

age (i.e. 30, 40, 50 or 90 days of age) a 4th instar locust was

introduced into its compartment for a five minute test. These intro-

ductions continued for six successive sessions with an inter-test

interval of two days. Thus, for example, subjects in the 30 Day Old

Table 5.1. Design of Experiment 1.

EXPERIMENTAL GROUP	AGES TESTED
30 DAY OLD	30 – 32 – 34 36 – 38 – 40
40 DAY OLD	40 – 42 – 44 46 – 48 – 50
50 DAY OLD	50 – 52 – 54 56 – 58 – 60
90 DAY OLD	90 – 92 – 94 96 – 98 – 100

group were tested at 30, 32, 34, 36, 38 and 40 days of age and

subjects in the 90 Day Old group were tested at 90, 92, 94, 96, 98

and 100 days of age. The design of this experiment is presented in

Table 5.1. Subjects which failed to capture within five minutes had

the locust removed (by the Experimenter) and the session terminated.

If a successful capture occurred within the allocated time subjects

were allowed an additional five minutes to eat the captured prey,

after which any remains were removed. The behaviours recorded via

a multiple pen records were exploration, withdrawal, nip, unsuccess-

ful capture and latency to capture. The amount of prey eaten, whether

or not the prey was pouched and if a subject carried the prey after

capture were also noted. In addition, the weight of all subjects

following the last test was taken. During the entire course of the

experiment subjects had **ad lib** access to food and water.

5.2.   RESULTS

5.2a.   General Treatment of the Data

Four points need mentioning here. First, in all cases the six

test sessions have been combined into three successive blocks of two

each. Statistical analysis was thus considerably simplified, even

though important information from the data might have been lost.

However, comparison of the data over the six test sessions with the

data after it had been blocked showed that very little information

was sacrificed. The trends, latencies to capture and the frequency

of the other behaviours on the six test sessions were similar to those

of the three test blocks. Thus, for example, subjects which failed

to capture on both sessions one and two were assigned the score of

600 seconds for block one. Likewise, subjects which made 14 explor-

ations on session three and seven on session four were accordingly

assigned the score of 21 explorations for block two.

The second point to note is that in most of the tables and

graphs the sexes from each age group have been combined. Again

this was done primarily to simplify the statistics; however, more

importantly, this was justified because inspection of the raw data

revealed no gross difference between the sexes in latency to capture

or the frequency of the other behaviours recorded. Therefore, on

block one, for example, the maximum average latency that could have

been achieved for any age group was 1200 seconds. That is, the

combination of test sessions one and two resulted in a maximum aver-

age latency of 600 seconds for block one and the further combination

of the latency scores of the males and females on this block doubled

the maximum latency to 1200 seconds. Frequency data for exploration,

withdrawal, nip and unsuccessful capture were treated in a similar

manner.

Third, latency to capture, the principal measure in the experi-

ment, represents the time interval from when the prey was introduced

into a subject's compartment to the first successful capture (i.e.

a 15 second hold on the locust). Whether or not latency scores should

have been based from the time when the initial exploration took place,

rather than that of the introduction, was a difficult matter to decide.

The latter was finally decided upon mainly because latencies to the initial exploration (i.e. the time it took a subject to detect the prey after it was introduced) were consistent among age groups (about 30 seconds) although the interval decreased somewhat on test sessions five and six.

Last, in most of the statistical tests only one tail of the normal distribution was used. One-tail tests were justified on the grounds of the implied directional hypothesis; namely, a decrease in latency to capture and the frequency of the other related behaviours with repeated testing. In the text where one-tail tests were used it is appropriately stated; where no mention of the direction of the test is made it should then be assumed that two-tail tests were employed.

5.2b. Loss of Subjects

Of the 112 subjects assigned to the four experimental groups 19 failed to complete testing. This occurred for two reasons; either because a subject died before the onset of testing or because it escaped from its compartment. All of those which escaped were from the 90 Day Old group (subjects M6, M13, F1) and of the sixteen who died, five were from the 30 Day Old group (subjects M5, M12, F5, F6, F14), two from the 40 Day Old group (subjects M11, F9), four from the 50 Day Old group (subjects F6, F9, F10, F13) and five from the 90 Day Old group (subjects M3, M11, F3, F4, F13). Altogether, 23 subjects from the 30 Day Old group completed testing (12 males and 11 females), 26 from the 40 Day Old group (13 males and 13 females),
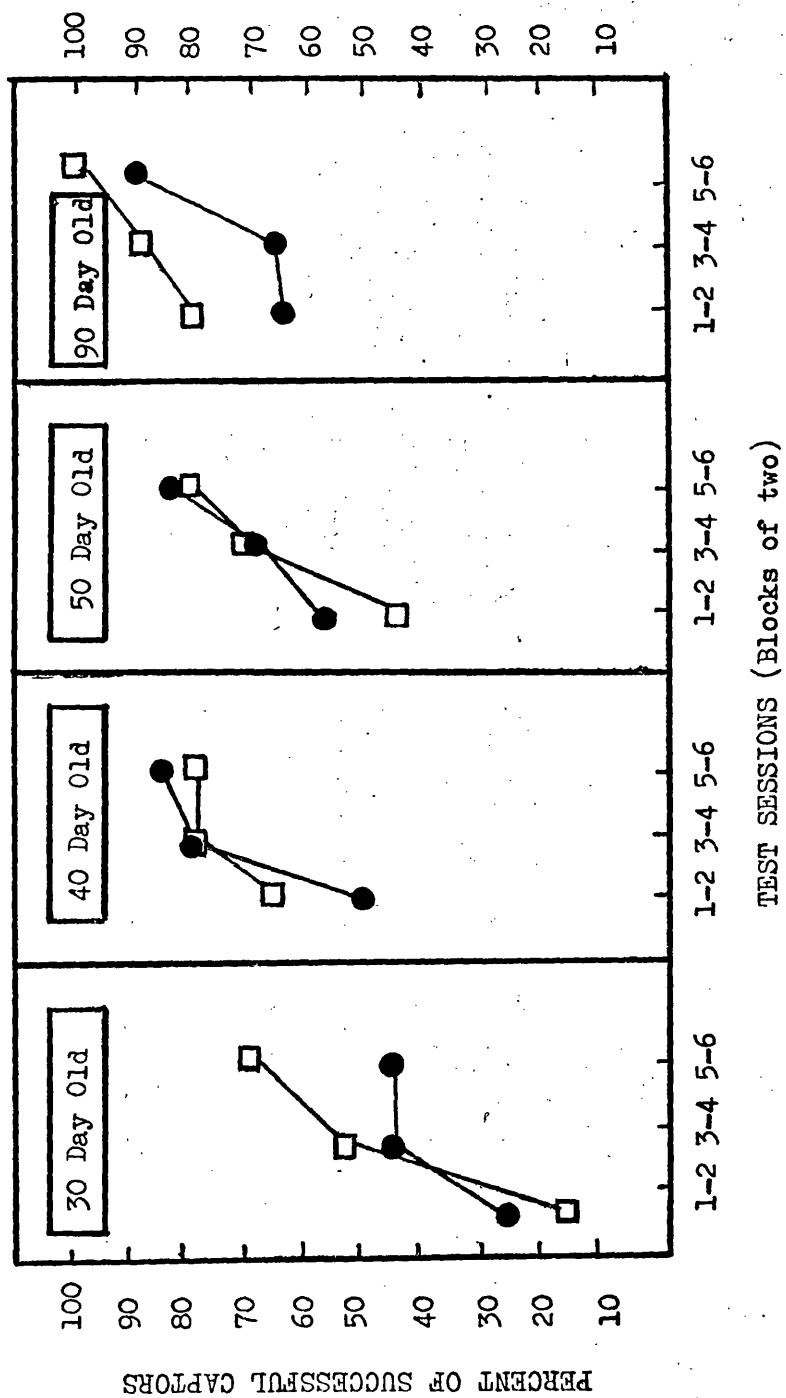
Figure 5.1. Percentage of successful locust captors in each age group. The number of captors in each age group have been combined into successive blocks of two. (□———□ male; ●———● female)
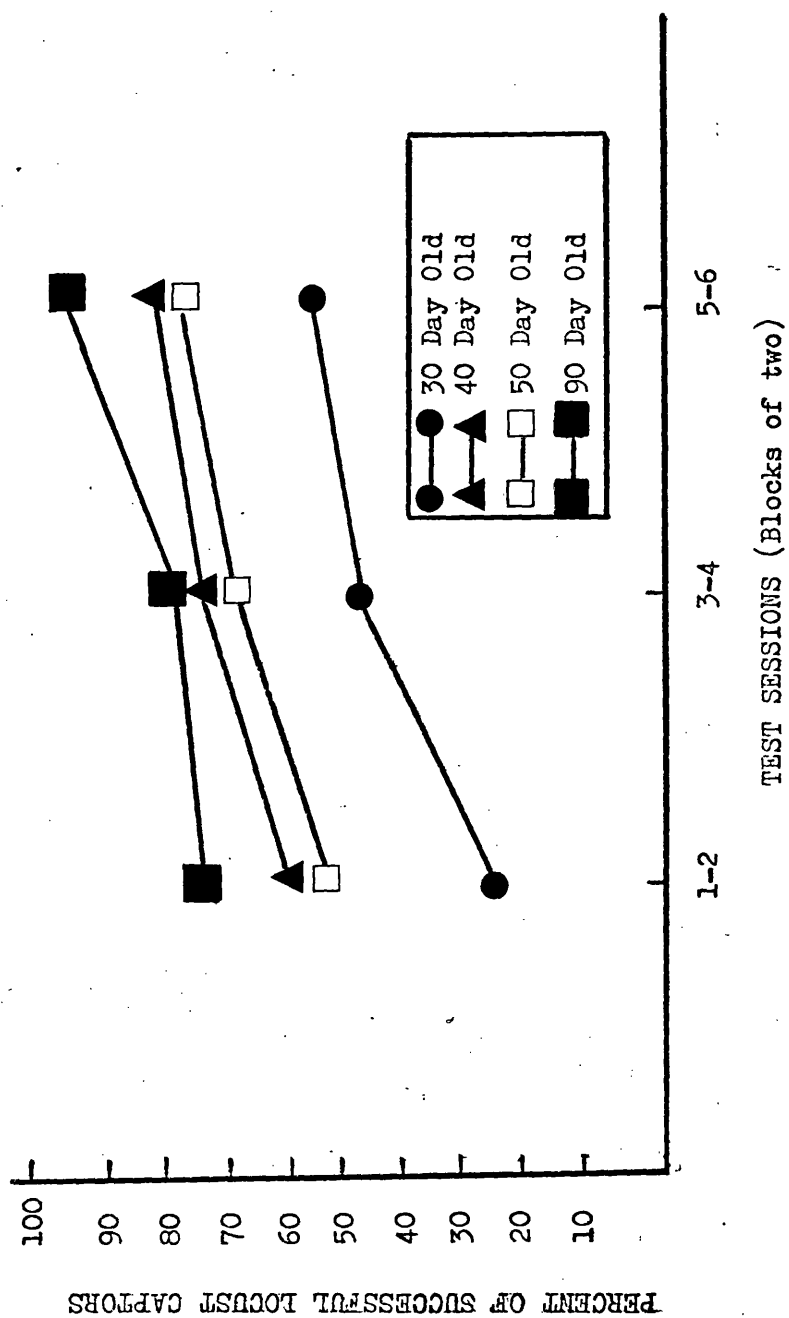
Figure 5.2. Percentage of successful locust captors in each age group, males and females combined. The number of captors in each age group have been combined into successive blocks of two.

Table 5.2. Z values based on the difference between the number of captors versus the number of non-captors for each test block as determined by the binomial test where p (the probability of capture) equals c (the probability of non-capture). Males and females within each age group have been combined. The figures in brackets under "C" and "NC" indicate the number of captors and non-captors, respectively, on any particular block. All probabilities are based on two-tailed tests.

AGE GROUP	TEST BLOCK 1		TEST BLOCK 2		TEST BLOCK 3	
	C	NC	C	NC	C	NC
30 Day Old (n = 23)	(5)	(18)	(11)	(12)	(13)	(10)
	-2.52^a		0		$.84$	
40 Day Old (n = 26)	(15)	(11)	(20)	(6)	(21)	(5)
	$.59$		2.55^a		2.95^b	
50 Day Old (n = 24)	(12)	(12)	(17)	(7)	(19)	(5)
	$.20$		1.84		2.66^b	
90 Day Old (n = 20)	(15)	(5)	(16)	(4)	(19)	(1)
	2.01^a		2.91^b		3.8^b	

[a] $p < .05$ [b] $p < .01$

Table 5.3. Chi Square values based on the
difference in the number of captors on the
successive test blocks as determined by the
McNemar test for the significance of changes,
corrected for continuity. Males and females within
each age group have been combined. The figure in
brackets under each test block refers to the number who
captured on any particular block. All probabilities are
based on one-tailed tests.

AGE GROUP	TEST BLOCK COMPARISONS		
	1 vs 2	1 vs 3	2 vs 3
30 Day Old	(5) (11) 4.16^a	(5) (13) 6.12^b	(9) (12) 1.33
40 Day Old	(15) (20) 4.80^a	(15) (21) 4.16^a	(20) (21) 0
50 Day Old	(12) (17) 3.2^a	(12) (19) 5.14^a	(17) (19) 1.0
90 Day Old	(15) (16) .5	(15) (19) 2.25	(16) (19) 1.33

[a] $p < .05$ [b] $p < .01$

24 from the 50 Day Old group (14 males and 10 females) and 20 from

the 90 Day Old group (10 males and 10 females).

5.2c.   Percentage of Captors

The percentage of subjects in each age group who captured

successfully on each test block is presented graphically in Figures

5.1 and 5.2.   Figure 5.1 differs from Figure 5.2 in that the sexes

in the latter have been combined.   Non-parametric analysis of this

data revealed no significant sex difference in any age group on any

test block as determined by the Fisher Exact Probability Test.   How-

ever, the ratio of captors to non-captors within each age group dif-

fered on most test blocks.   Table 5.2 depicts this relationship.

Inspection of this table shows that in the 30 Day Old group there

were significantly more non-captors on the first test block than

there were captors.   On test blocks two and three, though, there

were about as many captors as there were non-captors.   In the 40

Day Old group there were significantly more captors than non-captors

on test blocks two and three and this relationship also holds for the

50 Day Old group on test block three.   For the 90 Day Old group there

were significantly more captors than non-captors on all three test

blocks.

In Table 5.3 the number of captors on each test block are com-

pared directly.   In this table Chi Square values as determined by the

McNemar Test are presented.   Inspection shows that in all of the groups,

with the exception of the 90 Day Old group, there were significantly

Table 5.4. Number of captors/non-captors in each age group for each test block as determined by the Chi Square test for independent samples. Males and females within each age group have been combined. The figure in brackets indicates the proportion of subjects who captured in any particular age group. All probabilities are based on one-tailed tests.

AGE GROUP COMPARISONS

TEST BLOCK	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90
1	(27) (57) 8.10^c	(27) (50) 5.37^b	(27) (75) 14.43^c	(57) (50) .06	(57) (75) 2.35^a	(50) (75) 4.02^b
2	(47) (76) 5.78^c	(47) (70) 3.62^b	(47) (80) 6.21^c	(76) (70) .02	(76) (80) .37	(70) (80) 1.10
3	(56) (80) 4.61^b	(56) (79) 3.91^b	(56) (95) 10.46^c	(80) (79) .04	(80) (95) 3.46^b	(79) (95) 3.86^b

^{a} $p < .10$ ^{b} $p < .05$ ^{c} $p < .01$

more captors after the second or third test block than after the

first. In Figures 5.1 and 5.2 this linear trend upwards is clearly

illustrated for both sexes and the sexes combined.

In Table 5.4 the proportion of captors in each age group on

each test block are compared. Inspection shows that the 40, 50 and

90 Day Old groups had significantly more captors than the 30 Day Old

group on all three test blocks. Significant differences between the

90 Day Old and the 40 Day Old groups also emerged on test blocks one

and three but not on two. Further, no significance was present bet-

ween the 40 and 50 Day Old groups on any test block.

5.2d.   Latency to Capture

Due to the death of subjects the sample size between groups was

not equal. For this reason and in order to make the statistical

analysis far less complex three subjects were randomly selected from

the 30 Day Old group (M3, M6, M7), six from the 40 Day Old group (M4,

M7, M13, F3, F10, F12) and four from the 50 Day Old group (M1, M8, M13,

M14). No subject was discarded from the 90 Day Old group. This step

of randomly discarding the appropriate number of subjects from the

30, 40 and 50 Day Old groups equated the number of males and females

within the four groups (10 males and 10 females each); therefore

the latency data was amenable to a fairly straightforward parametric

test.

The raw latencies to capture over the six test sessions for all

Table 5.5. Means, variances and standard deviations of the scores for latency to capture for the males and females in each age group selected for statistical analysis in Experiment 1. The six test sessions have been combined into three successive blocks of two each. Latency scores are in seconds and all have been divided by 100.

AGE GROUP		TEST BLOCK					
		1		2		3	
		Male	Female	Male	Female	Male	Female
30 DAY OLD	M	5.17	5.23	4.64	4.46	3.26	4.15
	Var.	2.76	2.49	3.69	4.61	5.77	5.13
	S.D.	1.66	1.57	1.92	2.14	2.40	2.26
40 DAY OLD	M	4.91	4.97	3.19	3.09	2.23	2.69
	Var.	1.71	1.81	7.10	10.64	4.25	12.32
	S.D	1.30	1.34	2.66	3.26	2.06	3.50
50 DAY OLD	M	4.56	3.73	2.85	2.36	2.48	1.91
	Var.	2.54	4.69	4.82	5.76	3.75	4.93
	S.D.	1.59	2.16	2.19	2.40	1.93	2.22
90 DAY OLD	M	2.20	2.39	1.43	2.23	.95	2.42
	Var.	4.33	5.66	3.16	6.14	1.71	6.00
	S.D.	2.08	2.37	1.77	2.47	1.30	2.44
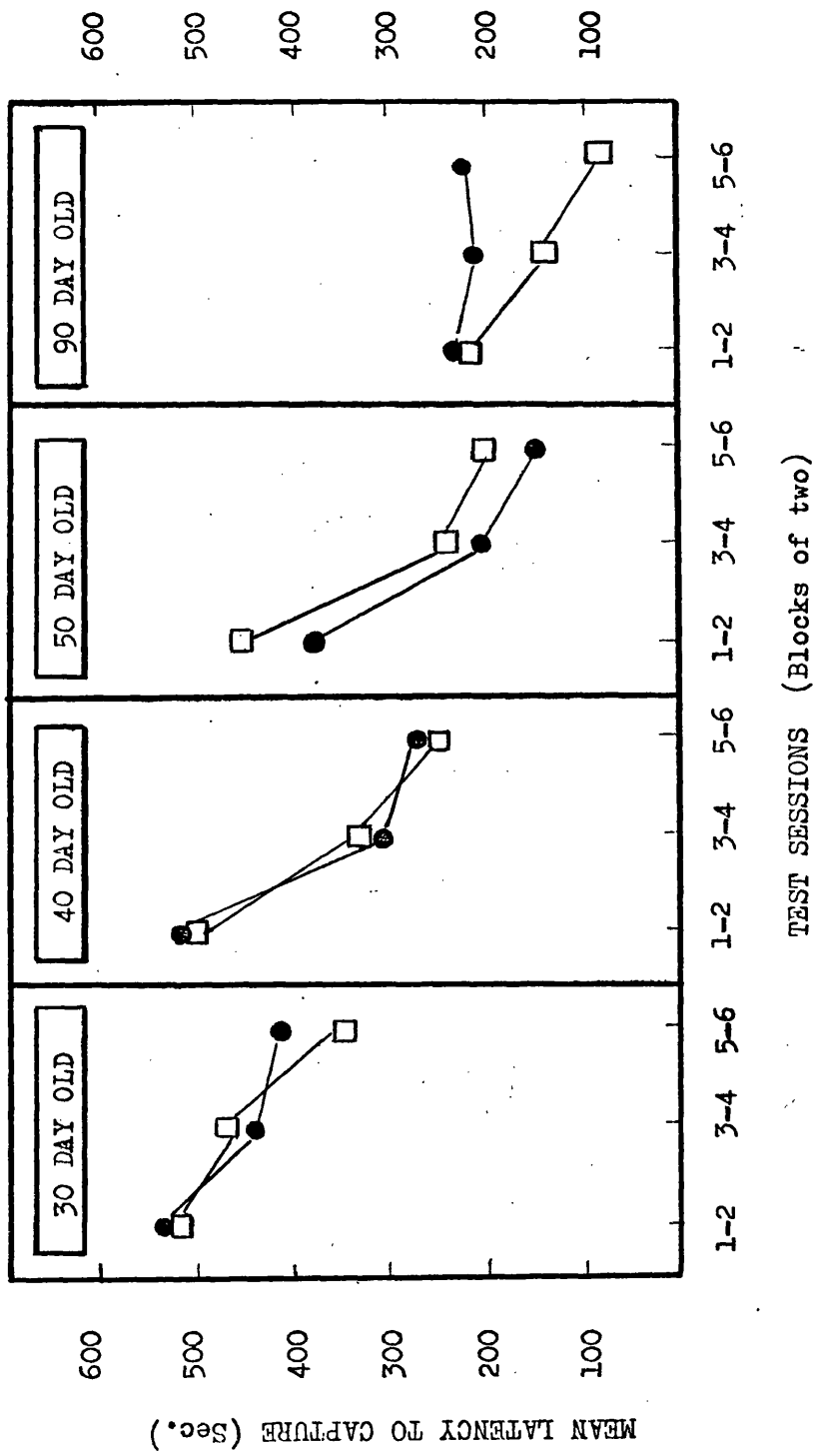
Figure 5.3. Mean delay between presentation and capture of a locust for each age group. The six test session have been combined into successive blocks of two. (□——□ males; ●——● females)
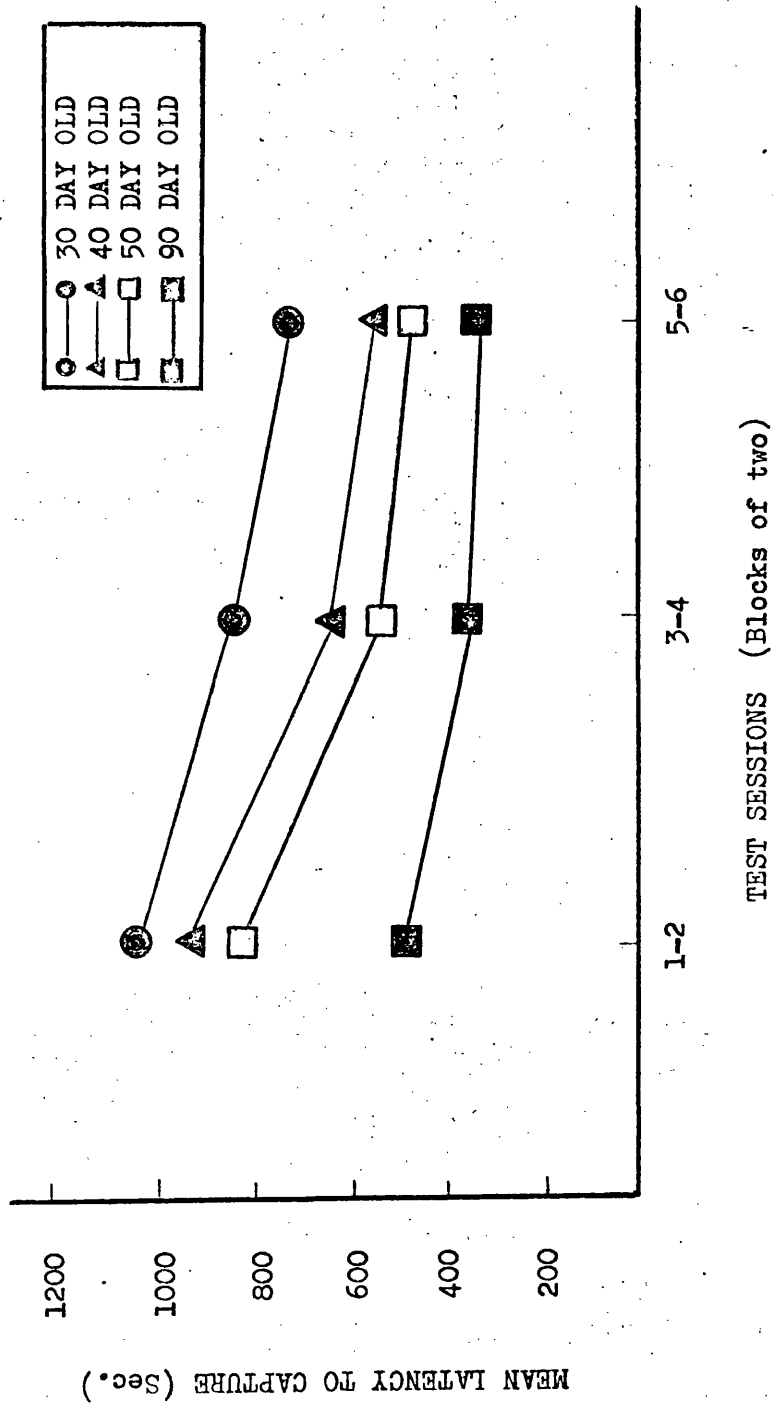
Figure 5.4. Mean delay between presentation and capture of a locust for each age group, males and females combined. The six test sessions have been combined into successive blocks of two.

Table 5.6. Summary of Analysis of Variance for latency to capture (Experiment 1).

SOURCE	SS	df	MS	F
Between A's (AGE)	199.3	3	66.43	5.37[b]
Between B's (SEX)	.39	1	.39	
A X B	21.11	3	7.03	
Between Conditions	220.8			
Between S's within conditions (error)	889.2	72	12.35	
Total between subjects	1110			
Total between trials	111.6	2	55.8	29.36[b]
A's X trials	23.61	6	3.93	2.06[a]
B's X trials	1.07	2	.53	
A's X B's X trials	.92	6	.15	
Conditions X trials	25.60			
Subjects X trials within conditions (error)	274.7	144	1.90	
Total subjects trials	300.3			
Grand total	1521.9	239		

[a] $p < .10$ [b] $p < .01$

subjects appear in Appendix B, Table 1. The mean latencies to capture, the variances and standard deviations for the 10 males and 10 females selected from each group are presented in Table 5.5. Latency scores in this table are in seconds and all have been divided by 100. The mean latency to capture for both sexes and for the sexes combined appear graphically in Figures 5.3 and 5.4. Inspection of Table 5.5 shows that all the variances and standard deviations within each group were roughly equal with the exception of the variance between the males and females of the 90 Day Old group on block three. A Hartley F max Test was conducted to determine if these two variances were homogeneous and the result showed that the probability of obtaining these two values by chance was greater than five per cent ($F = 3.50$, df $= 9$, $p > .05$); hence it was concluded that homogenity existed between them.

The parametric statistic used to analyse the latency data was a three factor analysis of variance with repeated measures, as outlined in Winer (1970, pp. 337 - 349). A summary of the analysis appears in Table 5.6. In accord with the non-parametric analysis, this analysis found no significant difference between the sexes in any age group on any test block. However, as indicated, significance emerged between age groups and between test blocks. The interaction between age groups and trials (i.e. test blocks) fell short of significance at the five per cent level with a two-tail test. With a one-tail test, however, this interaction was significant ($F = 2.06$, df $= 6/144$, $p < .05$).

Next, the reader should again examine Figures 5.3 and 5.4 which

Table 5.7. Summary of the Trend Analysis for latency to capture.

SOURCE OF VARIATION	SS	df	MS	F
Within Subjects (linear)	240.04	80		
C (trials)	107.38	1	107.38	71.58^{b}
AC (Age X trials)	18.66	3	6.22	4.14^{b}
BC (Sex X trials)	4.34	1	4.34	2.89^{a}
ABC	1.00	3	.33	δ
C X subj. W. groups	108.66	72	1.5	

$^{a}p < .10$ $^{b}p < .01$

illustrate a linear trend downward for latency to capture in all

age groups over the three test blocks. For example, the males and

females in the 40 Day Old group captured with an average latency of

491 seconds and 497 seconds on the first test block. On the third

test block, however, latency to capture was greatly reduced; the

males, on average, took 223 seconds, while the females had a some-

what higher but not significantly different latency of 269 seconds.[1]

In order to determine if the linear trend downward was signifi-

cant a trend analysis was conducted. A summary of this analysis

appears in Table 5.7. As expected, a highly significant linear trend

was obtained. A significant interaction between age and test blocks

also occurred; this indicates that the trend downward was significant

in some age groups but not in others. The interaction between sex and

test blocks fell short of significance at the five per cent level

(two-tail test).

Post-mortem tests were then conducted to pinpoint exactly where

significance occurred (i.e. between groups and between test blocks).

First, tests were conducted between the sexes in each age group for

each test block, and as the overall F score from the analysis of

variance indicated (Table 5.6), no significance was present on any

---

1. It should be remembered that the six test sessions have been
   combined to form three blocks of two each; hence the maximum
   score for the three test blocks in Figure 5.3 was 600 seconds
   and not 300 seconds. In Figure 5.4 the maximum latency for each
   block again doubles to 1200 seconds because latency scores for
   the sexes have been combined.

Table 5.8. T values based on the difference in latency to capture on the successive test blocks as determined by the t-test for related samples. Latency scores for the males and females within each age group have been combined. The figure in brackets within each cell indicates the mean latency to capture on the test blocks being compared. Latency scores have been divided by 100. All probabilities are based on one-tailed tests and the df= 19 for all test block comparisons.

	TEST BLOCK COMPARISONS		
AGE GROUP	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD	(10.4) (9.1) 2.69^b	(10.4) (7.4) 3.46^b	(9.1) (7.4) 2.60^b
40 DAY OLD	(9.8) (6.2) 5.03^b	(9.8) (4.9) 6.05^b	(6.2) (4.9) 2.30^a
50 DAY OLD	(8.2) (5.2) 4.02^b	(8.2) (4.3) 5.54^b	(5.2) (4.3) 1.60
90 DAY OLD	(4.5) (3.6) 2.61^b	(4.5) (3.3) 1.96^a	(3.6) (3.3) .70

^{a}p < .05 ^{b}p < .01

Table 5.9. Comparaison between the different age groups in terms of latency to capture on each of the three test blocks. The six test sessions have been combined into three successive blocks of two each. Latency scores for the males and females in each group have been combined. Figures in the brackets within each cell indicate the mean latency to capture for the two groups being compared and the unbracked figure indicates the difference between these means. Means are derived from raw latency scores which have been divided by 100. Values under the column labled "CR" indicate the critical range values at the .01 and .05 levels of significance as determined by the Tukey test. Any two means being compared differ significantly if their difference exceeds one of the critical range values. The difference between the means has been calculated on the basis of two decimal places.

AGE GROUP COMPARISONS

TEST BLOCK	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90	CR .05	CR .01
1	(10.4)(9.8) .52	(10.4)(8.2) 2.11^b	(10.4)(4.5) 5.81^b	(9.8)(8.2) 1.59^a	(9.8)(4.5) 5.29^b	(8.2)(4.5) 3.70^b	1.53	1.88
2	(9.1)(6.2) 2.82^b	(9.1)(5.2) 3.89^b	(9.1)(3.6) 5.44^b	(6.2)(5.2) 1.07	(6.2)(3.6) 2.62^b	(5.2)(3.6) 1.55	2.05	2.52
3	(7.4)(4.9) 2.49^a	(7.4)(4.3) 3.02^b	(7.4)(3.3) 4.04^b	(4.9)(4.3) .53	(4.9)(3.3) 1.55	(4.3)(3.3) 1.02	2.05	2.52

^{a} $p < .05$ ^{b} $p < .01$

test block. The only sex difference which might appear to be

significant through visual inspection of Figure 5.3 (Age Group 90,

block three) fell short of actual significance (t = 1.59, df = 18,

p < .20).

In Table 5.8, t values for all possible test block comparisons

within each age group are presented. As indicated, differences in

latency to capture between blocks one and two, two and three, and

one and three were significant in both the 30 and 40 Day Old groups.

In the 50 and 90 Day Old groups significance existed between blocks

one and two, and one and three, but not between two and three.

The Tukey test was then conducted for all possible age group

comparisons on each test block and the results appear in Table 5.9.

Inspection shows that on block one the 30 Day Old group had a sig-

nificantly higher latency to capture than the 50 or 90 Day Old groups.

Further, the 40 Day Old group differed significantly from age groups

50 and 90, and the 50 Day Old group differed significantly from the

90 Day Old group. On test block two significance existed between

all groups with the exception of age groups 40 and 50, and 50 and

90. On test block three the 30 Day Old group differed significantly

from all groups; no significance was present, however, between age

groups 40 and 50, 40 and 90, and 50 and 90.

Up to this point, analysis of the latency data has been per-

formed on the scores of 20 subjects randomly selected from three of

the four age groups. Within each group, however, there were subjects

who failed to capture, as Figures 5.1, 5.2 and Table 5.2 indicate.

Thus, the latency scores which have been analysed so far have taken

into account the scores of the captors as well as the non-captors.

As already stated non-captors were assigned the score of 300 seconds

for each session they failed to capture and adding in these scores

with those of the captors might well have inflated significance between

the groups. For example, the fact that the 30 Day Old group had a

significantly higher latency to capture than the 90 Day Old group

(see Figure 5.4) may have been due simply to the fact that they had

more non-captors (see Figure 5.2). In effect, then, the combination

of the latency scores of the captors with the scores of the non-

captors could have masked whatever differences there might have been

between the captors only, and it is possible that the captors of the

30 Day Old group differed in no significant way from the captors of

the other three age groups. To examine this possibility and in order

to get a more representative picture of how a captor's behaviour

changed with repeated testing, it seemed desirable to analyse the

latency scores of only those who captured.

Therefore, the analysis reported below was conducted on the

scores of those subjects who captured on at least five of the six

test sessions. Five subjects from the 30 Day Old group met this

criterion (M2, M9, F2, F8, F9), thirteen from the 40 Day Old group,

(M3, M5, M7, M10, M13, M14, F1, F4, F10, F11, F12, F13, F14), and

twelve from the 50 Day Old group (M3, M5, M7, M8, M9, M10, F2, F3,

F4, F7, F10, F11). In the 90 Day Old group every subject captured

on at least five of the six test sessions with the exception of M1,

M4, F2, F5, and F7.

Table 5.10. The mean, variance, and standard deviation for latency to capture for those subjects in each age group who captured on at least five of the six test sessions, males and females combined. The six test sessions have been combined into three successive blocks of two each. Latency scores have been transformed into their log equivalents.

	TEST BLOCK		
AGE GROUP	1	2	3
30 DAY OLD			
(n = 5) M	2.38	2.06	2.01
VAR.	.080	.027	.020
S.D.	.89	.16	.44
40 DAY OLD			
(n = 13) M	2.40	1.81	1.75
VAR.	.188	.197	.088
S.D.	.43	.44	.29
50 DAY OLD			
(n = 12) M	2.34	1.84	1.83
VAR.	.107	.144	.080
S.D.	.327	.379	.89
90 DAY OLD			
(n = 15) M	1.96	1.74	1.74
VAR.	.071	.059	.067
S.D.	.26	.24	.25

185.
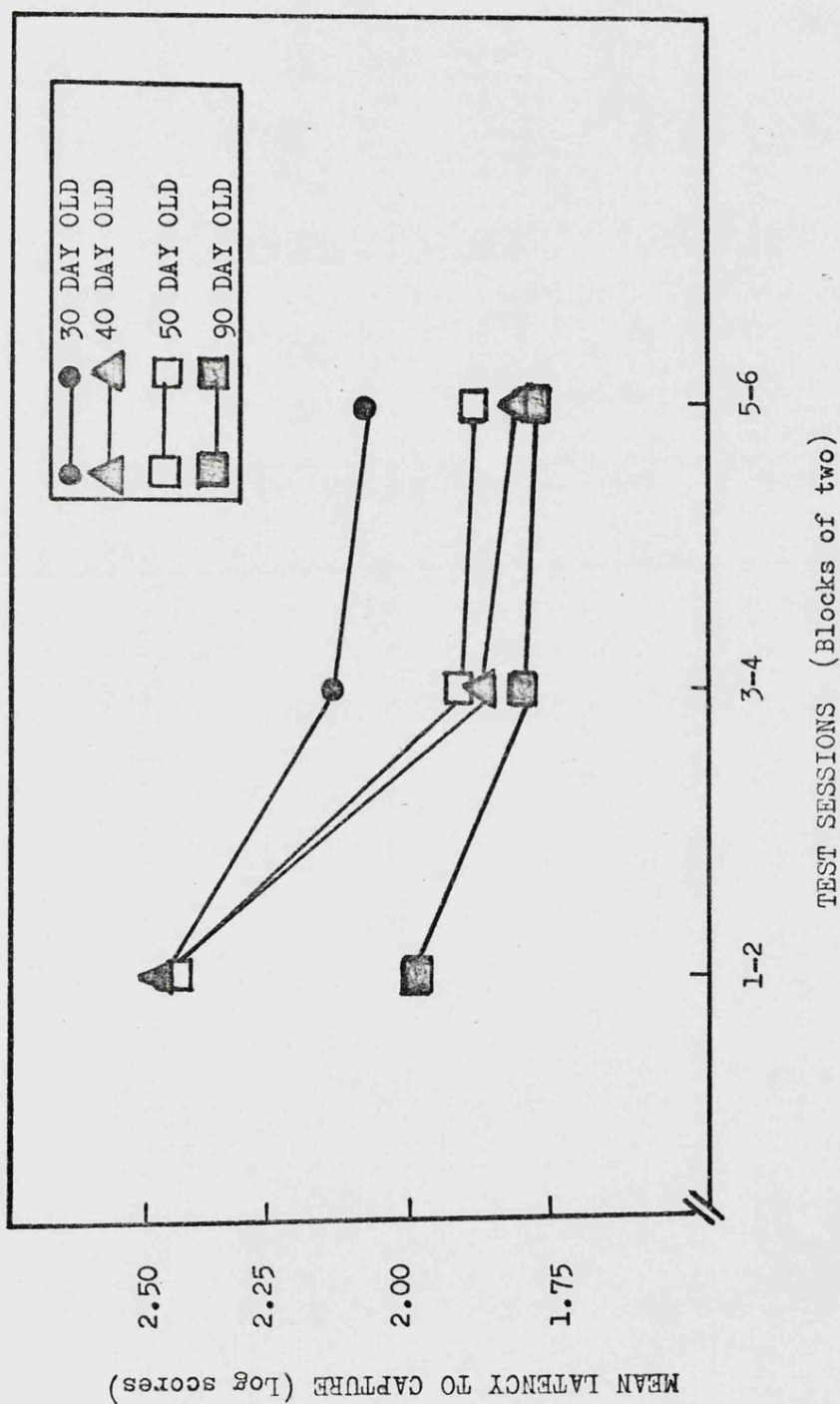
Figure 5.5   Mean delay between presentation and capture of a locust for those subjects in each age group who captured on at least five of the six test sessions, males and females combined. The six test sessions have been combined into three successive blocks of two each.

Table 5.11. Summary of the analysis of variance for the captors of Experiment 1.

SOURCE OF VARIATION	SS	df	MS	F
Between subjects		44		
A (age)	1.49	3	.49	6.12[a]
Subjects w. groups	3.42	41	.08	
Within subjects		90		
B (trials)	4.40	2	2.20	23.40[a]
AB (age X trials)	.28	6	.04	.44
B X subjects w. groups	7.78	82	.09	

[a] $p < .01$

Table 5.12. T values based on the difference in
latency to capture on three successive test blocks for
those subjects in each age group who captured on at
least five of the six test sessions as determined by
the t- test for related samples. The six test sessions
have been combined into three successive blocks of two
each. Males and females within each age group have
been combined. The figure in brackets within each cell
indicates the mean latency to capture on the test blocks
being compared. Latency scores have been transformed
into their log equivalents. All probabilities are based
on one-tailed tests.

| | TEST BLOCK COMPARISONS | | |
AGE GROUP	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD (n = 5)	(2.3) (2.0) 4.77^b	(2.3) (2.0) 3.52^a	(2.0) (2.0) .52
40 DAY OLD (n = 13)	(2.4) (1.8) 4.12^b	(2.4) (1.7) 8.00^b	(1.8) (1.7) .37
50 DAY OLD (n = 12)	(2.3) (1.8) 9.08^b	(2.3) (1.8) 8.38^b	(1.8) (1.8) .15
90 DAY OLD (n = 15)	(1.9) (1.7) 3.22^b	(1.9) (1.7) 2.81^b	(1.9) (1.7) .15

[a] $p < .025$ [b] $p < .01$

Table 5.13. Comparison between the different age groups in terms of latency to capture. The six test sessions have been combined into three successive blocks of two each. The figure in brackets within each cell indicates the mean latency to capture for the groups being compared and the unbracketed figure indicates the difference between these means. Latency scores have been transformed into their log equivalents. All means are based on latency scores of only those subjects who captured on at least five of the six test sessions. Males and females within each age group have been combined. Values under the column labled "CR" indicate the critical range values at the .01 and .05 levels of significance as determined by the Tukey test. Latency scores within the brackets differ significantly if their difference exceeds one of the critical range values. The difference between the means has been calculated on the basis of two decimal places.

TEST BLOCK	AGE GROUP COMPARISONS						CR	
	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90	.05	.01
1	(2.3) (2.4) .04	(2.3) (2.3) .04	(2.3) (1.9) .42^a	(2.4) (2.3) .06	(2.4) (1.9) .44^a	(2.3) (1.9) .38^a	.37	.47
2	(2.0) (1.8) .25	(2.0) (1.8) .22	(2.0) (1.9) .32	(1.8) (1.8) .03	(1.8) (1.7) .07	(1.8) (1.7) .10	.37	.47
3	(2.0) (1.9) .26	(2.0) (1.8) .18	(2.0) (1.7) .27	(1.7) (1.8) .08	(1.7) (1.7) .01	(1.8) (1.7) .11	.30	.37

^{a} p < .05

Inspection of the raw data revealed no gross sex difference in latency to capture between the male and female captors; because of this, males and females within each group were combined. Further, due to the lack of homogenity of the raw data, all latency scores were transformed into their log equivalents. Test sessions, as in the analysis above, were combined into three successive blocks of two each.

Table 5.10 presents the mean latencies to capture, the variances and standard deviations for the captors of each group. In Figure 5.5 the mean latencies to capture over three successive test blocks are graphically presented and a summary of the analysis of variance appears in Table 5.11. The results of this analysis show a highly significant difference between age groups and between test blocks (i.e. trials); however, the F value for the age x trials interaction was nowhere near as great as it was when both captors and non-captors were included in the same analysis (F values of 2.06 and .44 respectively).

Post-mortem analysis of this data is presented in Tables 5.12 and 5.13. Inspection of Table 5.12 shows that significant differences occurred between test blocks one and two, and one and three for all groups. On the other hand, no significance was present in any of the groups between test blocks two and three. Between-group analysis revealed marginal significance between the 90 Day Old group and the other three age groups on test block one, as Table 5.13 indicates; however, no significance was present between any group on test blocks two and three.

5.2e.   Frequency of Exploration, Withdrawal, Nip and Unsuccessful

        Capture

      Statistical analysis of the other behaviours recorded in this

experiment will be presented in two parts. In the first, the analy-

sis scrutinizes the cumulative frequency of each behaviour prior to

the initial capture. This was scored in the following manner: for

example, if a subject's initial capture occurred on test session

four, then all the explorations, withdrawals, nips and unsuccessful

captures it made on test sessions one, two, three and four were

summed to determine the cumulative frequency. Specifically, take

the case of M7 of the 30 Day Old group in terms of the number of

explorations it made prior to the initial capture (see Appendix B,

Table 2 for the raw data). The initial capture for this subject

occurred on test session five (see Appendix B, Table 1). Prior to

this it made four explorations on session one, 13 on session two,

eight on session three, six on session four and one exploration on

session five (the session on which it captured) for a cumulative total

of 32 explorations prior to the initial capture. The cumulative

totals for all subjects within an age group were then pooled for each

of the four behaviours in order to derive a mean cumulative total for

each behaviour.

      Following this, analysis of the frequency of each of these

behaviours per test session will be presented. Test sessions were

again blocked in groups of two, and the frequency scores of males

and females within each group were combined. Further, this analysis

Table 5.14. The mean, variance, and standard deviation for the
cumulative frequency of exploration, withdrawal, nip and
unsuccessful capture prior to the initial capture for the subjects
in Experiment 1.

AGE GROUP		BEHAVIOUR			
		EXPLOR.	WITHDRAWAL	NIP	U. CAPTURE
30 DAY OLD (n = 13)	M	37.9	14.3	13.7	6.69
	VAR.	455.75	82.91	64.25	31.91
	S.D.	21.34	9.10	8.01	5.64
40 DAY OLD (n = 22)	M	26.4	9.4	7.8	3.09
	VAR.	249.9	88.76	31.42	9.04
	S.D.	15.80	9.42	5.60	3.00
50 DAY OLD (n = 19)	M	25.9	8.7	5.1	1.78
	VAR.	376.94	111.88	10.61	2.00
	S.D.	19.41	10.57	3.25	1.41
90 DAY OLD (n = 19)	M	15.5	1.5	5.2	1.42
	VAR	506.94	5.92	15.66	2.61
	S.D.	22.51	2.43	3.95	1.61
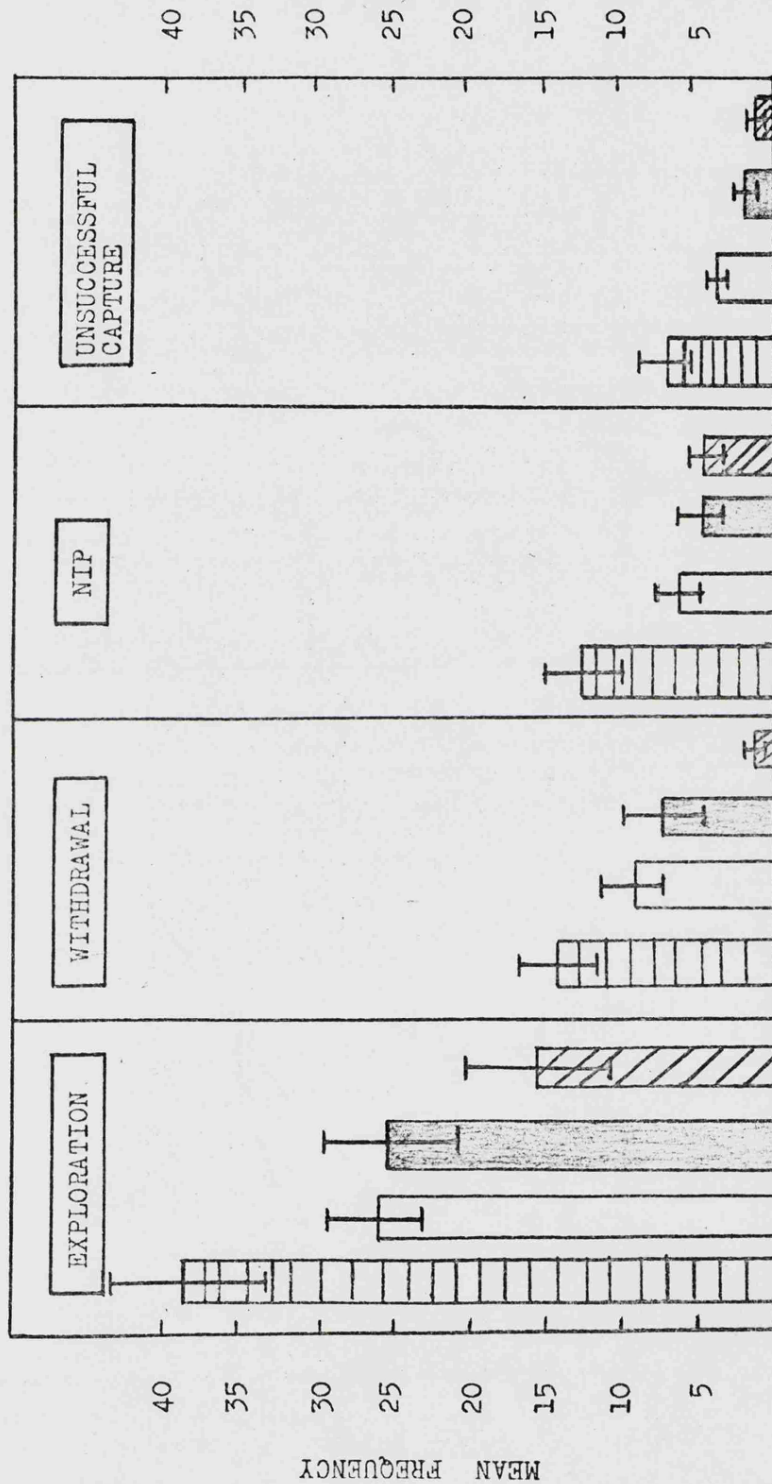
Figure 5.6. Mean frequency of exploration, withdrawal, nip, and unsuccessful capture prior to the initial capture for those subjects in each age group, males and females combined. Vertical bars represent the standard error of the mean. (□ 30 DAY OLD; □ 40 DAY OLD; ▨ 50 DAY OLD; ▨ 90 DAY OLD)

was made on the frequency scores of only those subjects who captured

on at least five of the six test sessions. Exclusion of the non-

captors (i.e. those who failed to capture or who captured only once)

was necessary because they rarely nipped or attempted capture, and

preliminary analysis of the data showed that inclusion of the non-

captors with the captors obscured the obvious decrease in frequency

which occurred with repeated testing. Analysis of the non-captors

exploratory and withdrawal behaviour will be treated separately in

Section 5.2j.

The raw frequency of exploration, withdrawal, nip and unsuccess-

ful capture for all subjects appears in Appendix B, Table 2, Table 3,

Table 4 and Table 5.

Cumulative Frequency Prior to the Initial Capture

To be included in this analysis a subject had to make at least

one capture in the six times it was tested. This criterion was ful-

filled by thirteen subjects from the 30 Day Old group, twenty-two from

the 40 Day Old group and nineteen subjects from both the 50 and 90

Day Old groups.[2] The mean frequency of each of these behaviours, the

variances and standard deviations appear in Table 5.14. In addition,

the means are presented graphically in Figure 5.6. On average, as

shown, subjects in the 30 Day Old group made approximately 38 explor-

ations prior to the initial capture. On the other hand, subjects in

---

2. Consult the raw latency scores in Appendix B, Table 1 in order to
   determine the subjects that met this criterion.

TABLE 5.15. Summary of the Kruskal-Wallis one-way
analysis of variance for the cumulative frequency of
exploration, withdrawal, nip, and unsuccessful
capture prior to the initial capture for the subjects
of Experiment 1.

BEHAVIOUR	H VALUE	df	PROBABILITY
EXPLORATION	14.95	3	< .01
WITHDRAWAL	25.00	3	< .001
NIP	14.44	3	< .01
U. CAPTURE	18.76	3	< .001

the 90 Day Old group made about half as many (mean of 15.5). The

90 Day Old group also showed an exceptionally low incidence of

withdrawal behaviour (mean of 1.5 prior to the initial capture)

when compared with the other three age groups (nearly ten times

as many for the 30 Day Old group). The cumulative total of nip

was also greater for the younger age groups (mean of 13.7 and 7.8

for the 30 and 40 Day Old groups; this compares with a mean of

5.1 for the 50 Day Old group and a mean of 5.2 for the 90 Day Old

group). With regard to the cumulative frequency of unsuccessful

capture, the 30 Day Old group made more than twice as many unsuc-

cessful captures as the 40 Day Old group (6.6 vs. 3.0) and about

four times as many as the 50 and 90 Day Old groups (cumulative mean

totals of 1.78 and 1.42).

A Kruskal-Wallis one-way analysis of variance was performed to

test for significance between age groups for each of the four behav-

iours, and a summary of the results appears in Table 5.15. Inspec-

tion shows that highly significant differences were obtained between

the groups for all behaviours.

Frequency per Test Session

The subjects included in this analysis have already been listed

(see results in Section 5.2d, captors only). Again, though, they

were those subjects who met the criterion of capture on at least five

of the six test sessions. The mean frequency, the variance and the

standard deviation for each of the four behaviours per test block are

Table 5.16. Means, variances and standard deviations for the frequency of explorations, withdrawals, nips, and unsuccessful captures on each of the three test blocks for those subjects in each age group who captured on at least five of the six test sessions. Frequency scores for those subjects who failed to capture on at least five of the six test sessions are not included. The six test sessions have been combined into three successive blocks of two each. Frequency scores for the males and females in each age group have been combined.

TEST BLOCK

AGE GROUP		E	W	N	U.C.	E	W	N	U.C.	E	W	N	U.C.
			1				2				3		
30 DAY OLD (n = 5)	M	21.2	10.0	13.2	5.8	9.2	1.6	7.0	3.6	8.8	2.2	3.6	2.2
	VAR.	26.1	41.6	28.9	.56	13.3	2.6	7.2	3.4	29.3	11.6	3.4	6.1
	S.D.	5.1	6.4	5.3	.74	3.6	1.6	2.6	1.8	5.4	3.4	1.8	2.4
40 DAY OLD (n = 13)	M	21.7	5.5	9.4	4.4	10.0	1.5	5.8	2.0	5.4	.38	3.6	1.3
	VAR.	129.1	45.6	20.4	25.8	86.0	8.4	9.2	3.3	8.1	.86	1.7	3.7
	S.D.	11.3	6.8	4.5	5.0	9.2	2.9	3.0	1.8	2.8	.92	1.3	1.9
50 DAY OLD (n = 12)	M	19.5	4.3	7.8	2.9	6.8	.75	4.0	2.0	5.8	.66	3.7	1.3
	VAR.	171.4	19.4	16.2	10.7	11.2	2.1	4.2	2.5	24.0	1.0	4.6	3.0
	S.D.	13.0	4.4	4.0	3.2	3.3	1.4	2.0	1.6	4.9	1.0	2.1	1.7
90 DAY OLD (n = 15)	M	7.8	.66	6.2	1.8	3.6	0	2.7	.40	3.0	0	2.9	.40
	VAR.	21.9	.90	9.8	3.6	2.9	0	.88	.77	1.8	0	1.5	.37
	S.D.	4.6	.94	3.1	1.9	1.7	0	.93	.87	1.36	0	1.2	.60

TEST SESSIONS (Blocks of two)
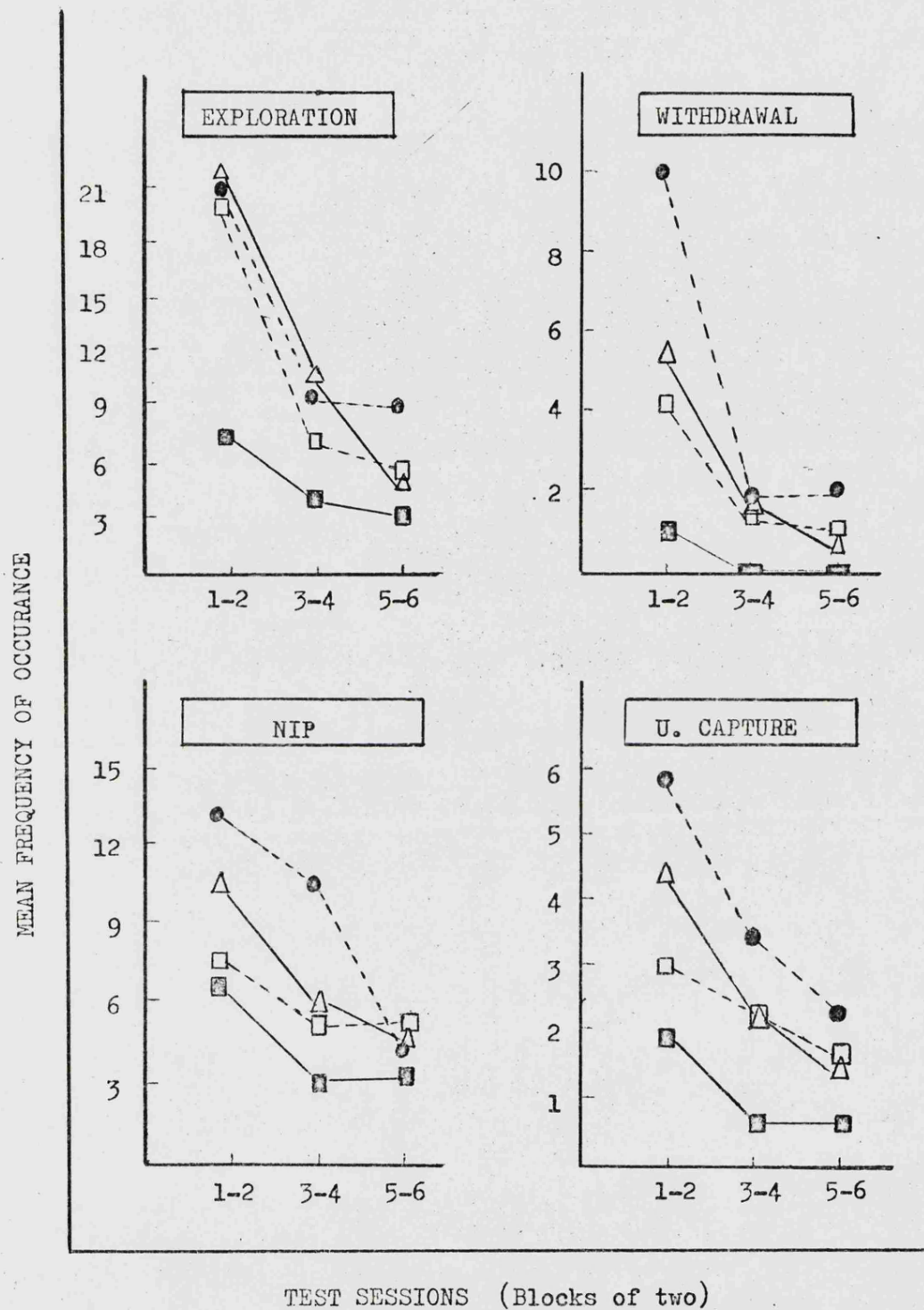
Figure 5.7. Mean frequency of exploration, withdrawal, nip, and unsuccessful capture for those subjects in each age group who captured on at least five of the six test sessions. Frequency scores for those subjects who failed to capture on at least five of the six test sessions are not included. Males and females in each age group have been combined and the sessions have been grouped into three successive blocks of two each. (○------○ 30 DAY OLD; △——△ 40 DAY OLD; □----□ 50 DAY OLD; ▢——▢ 90 DAY OLD)

Table 5.17. Comparison in terms of the number of explorations on any two test blocks for those subjects in each age group who captured on at least five of the six test sessions. The six test sessions have been combined into three successive blocks of two each. The figure in brackets within each cell indicates the mean frequency of occurrence and the unbracketed figure indicates the probability that the two means being compared differ significantly from each other as determined by the Sign Test where $p=q=\frac{1}{2}$. Frequency scores for the males and females within each group have been combined. All probabilities are based on one-tailed tests.[a]

	TEST BLOCK COMPARISONS		
AGE GROUP	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD (n = 5)	(21.2) (9.2) .97	(21.2) (8.8) .96	(9.2) (8.8) .50
40 DAY OLD (n = 13)	(21.7)(10.0) .98	(21.7) (5.4) .99	(10.0) (5.4) .91
50 DAY OLD (n = 12)	(19.5) (6.8) .99	(19.5) (5.8) .99	(6.8) (5.8) .88
90 DAY OLD (n = 15)	(7.8) (3.6) .98	(7.8) (3.0) .98	(3.6) (3.0) .88

[a]Probability values listed are the inverse of those values listed in Table D of Siegel (1956, p- 250)

Table 5.18. Comparison in terms of the number of withdrawals
on any two test blocks for those subjects in each age group
who captured on at least five of the six test sessions. Test
sessions have been grouped into three successive blocks of
two each. The figure in brackets within each cell indicates the
mean frequency of occurrence and the unbracketed figure
indicates the probability that the two means being compared
differ significantly from each other as determined by the Sign Test
where p=q=1/2. Frequency scores for the males and females
within each age group have been combined. All probabilities
are based on one-tailed tests.[d]

	TEST BLOCK COMPARISONS		
AGE GROUP	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD (n = 5)	(10.0) (1.6) .97	(10.0) (2.2) .95[a]	(1.6) (2.2) .55[b]
40 DAY OLD (n = 13)	(5.5) (1.5) .99	(5.5) (.38) .99	(1.5) (.38) .82
50 DAY OLD (n = 12)	(4.3) (.75) .98	(4.3) (.66) .99	(.75) (.66) .60[c]
90 DAY OLD (n = 15)	(.66) (0) .99	(.66) (0) .99	(0) (0) NS

[a]
Sample size too small for analysis by Sign Test, hence
probability determined by one-tailed t-test for related
samples (t= 2.16, df= 4, p < .05)

[b]
Sample size too small for analysis by Sign Test, hence
probability determined by one-tailed t-test for related
samples (t= .09, df= 4, p > .45)

[c]
Sample size too small for analysis by Sign Test, hence
probability determined by one-tailed t-test for related
samples (t= .25, df= 11, p > .40)

[d]Probability values listed are the inverse of those values
listed in Table D of Siegel (1956, p-250)

Table 5.19. Comparison in terms of the number of nips on any two test blocks for those subjects in each age group who captured on at least five of the six test sessions. Test sessions have been grouped into three successive blocks of two each. The figure in brackets within each cell indicates the mean frequency of occurrence and the unbracketed figure indicates the probability that the two means being compared differ significantly from each other as determined by the Sign Test where p=q=1/2. Frequency scores for the males and females within each age group have been combined. All probabilities are based on one-tailed tests.[b]

AGE GROUP	TEST BLOCK COMPARISONS		
	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD (n = 5)	(13.2) (7.0) .82	(13.2) (3.6) .98[a]	(7.0) (3.6) .97
40 DAY OLD (n = 13)	(9.4) (5.8) .93	(9.4) (3.6) .99	(5.8) (3.6) .99
50 DAY OLD (n = 12)	(7.8) (4.0) .99	(7.8) (3.7) .99	(4.0) (3.7) .75
90 DAY OLD (n = 15)	(6.2) (2.7) .99	(6.2) (2.9) .99	(2.7) (2.9) .95

a
Sample size too small for analysis by Sign Test, hence probability determined by one-tailed t-test for related samples (t= 3.15, df= 4, p < .025).

b
Probability values listed are the inverse of those values listed in Table D of Siegel (1956, p- 250).

Table 5.20. Comparison in terms of the number of unsuccessful captures on any two test blocks for those subjects in each age group who captured on at least five of the six test sessions. Test sessions have been grouped into three successive blocks of two each. The figure in brackets within each cell indicates the mean frequency of occurrence and the unbracketed figure indicates the probability that the two means being compared differ significantly from each other as determined by the Sign Test where p=q=1/2. Frequency scores for the males and females within each group have been combined. All probabilities are based on one-tailed tests.[c]

	TEST BLOCK COMPARISONS		
AGE GROUP	1 vs 2	1 vs 3	2 vs 3
30 DAY OLD (n = 5)	(5.8) (3.6) .98[a]	(5.8) (2.2) .82[b]	(3.6) (2.2) .82
40 DAY OLD (n = 13)	(4.4) (2.3) .73	(4.4) (1.3) .99	(2.3) (1.3) .95
50 DAY OLD (n = 12)	(2.9) (2.0) .50	(2.9) (1.3) .95	(2.0) (1.3) .97
90 DAY OLD (n = 15)	(1.8) (.4) .99	(1.8) (.4) .99	(.4) (.4) .27

[a]
Sample size too small for analysis by Sign Test, hence probability determined by one-tailed t-test for related samples (t= 3.01, df= 4, p < .025).

[b]
One-tailed t-test for related samples did yield significance, however, between these two blocks (t= 3.10, df= 4, p < .025).

[c]Probability values listed are the inverse of those values listed in Table D of Siegel (1956, p-250).

presented in Table 5.16. Graphical presentation of the means appears

in Figure 5.7. Examination of Figure 5.7 clearly shows that the fre-

quency of each behaviour decreased in all groups with repeated testing.

Further, for each behaviour the 90 Day Old group had a lower frequency

than the 30 Day Old group and in most cases a lower frequency than

either the 40 or 50 Day Old group. The 40 and 50 Day Old groups,

in turn, each had a lower frequency than the 30 Day Old group on all

behaviours.

In an attempt to pinpoint where significance occurred (between

test blocks and between age groups) the data were analysed with the

non-parametric Sign Test and the non-parametric Mann-Whitney U Test.

Results of the Sign Test analysis (for difference between test blocks)

appear in Table 5.17 for exploration, Table 5.18 for withdrawal,

Table 5.19 for nip and Table 5.20 for unsuccessful capture. Each

table lists the probability that the two means being compared differ

significantly from each other. Table 5.17 shows that the frequency

of exploration was significantly lower both on blocks two and three

than on one for all age groups. However, no significance was present

between blocks two and three in any group. Withdrawal behaviour

decreased in similar fashion as Table 5.18 indicates; that is, all

groups had significantly fewer withdrawals on blocks two and three

than on block one. Table 5.19 shows that all groups nipped fewer

times with repeated testing; however, the decrease in this behaviour

was not as straightforward as was the case for exploration and with-

drawal. For example, for all groups there were significantly fewer

nips on block three than on block one and the only significance present

Table 5.21. Comparison between the different age groups in terms of number of explorations on each of the six test sessions. Test sessions have been combined into three successive blocks of two each. The figure in brackets within each cell indicates the mean number of explorations for the two groups being compared and the unbracketed figure indicates their respective U score as determined by the Mann-Whitney U Test. All means and U scores are based on the frequency scores of only those subjects who captured on at least five of the six test sessions. Males and females within each age group have been combined. All probabilities are based on one-tailed tests.

AGE GROUP COMPARISONS

TEST BLOCK	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90
1	(21.2)(21.7) 30	(21.2)(19.5) 21	(21.2)(7.8) 2.5 [b]	(21.7)(19.5) 91	(21.7)(7.8) 17 [b]	(19.5)(7.8) 33 [b]
2	(9.2)(10.0) 26.5	(9.2)(6.8) 20	(9.2)(3.6) 7 [b]	(10.0)(6.8) 68.5	(10.0)(3.6) 39 [b]	(6.8)(3.6) 30.5 [b]
3	(8.8)(5.4) 22	(8.8)(5.8) 19.5	(8.8)(3.0) 12 [a]	(5.4)(5.8) 69.5	(5.8)(3.0) 35.5 [b]	(5.8)(3.0) 47 [a]

[a] $p < .025$ [b] $p < .01$

Table 5.22. **Comparison** between the different age groups in terms of number of withdrawals on each of the six test sessions. Test sessions have been combined into three successive blocks of two each. Figures in the brackets within each cell indicate the mean number of withdrawals for the two groups being compared and the unbracketed figure indicates their respective U score as determined by the Mann-Whitney U Test. All means and U scores are based on the frequency scores of only those subjects who captured on at least five of the six test sessions. Males and females within each age group have been combined. All probabilities are based on one-tailed tests.

TEST BLOCK	AGE GROUP COMPARISONS					
	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90
1	(10.0) (5.3) 18.5	(10.0) (4.3) 12 [a]	(10.0)(.66) 4.5 [c]	(5.5) (4.3) 74	(5.5) (.66) 33.5 [c]	(4.3) (.66) 38.5 [c]
2	(1.6) (1.5) 26.5	(1.6) (.75) 20.5	(1.6) (0) 15 [a]	(1.5) (.75) 50.5	(1.5) (0) 52.5 [b]	(.75) (0) 67.5
3	(2.2) (.38) 18.5	(2.2) (.66) 21.5	(2.2) (0) 15 [a]	(.38) (.66) 65.5	(.38) (0) 82.5	(.66) (0) 60.0

[a] $p < .05$ [b] $p < .025$ [c] $p < .01$

Table 5.23. Comparison between the different age groups in terms of number of nips on each of the six test sessions. Test sessions have been combined into three successive blocks of two each. Figures in the brackets within each cell indicate the mean number of nips for the two groups being compared and the unbracketed figure indicates their respective U score as determined by the Mann-Whitney U Test. All means and U scores are based on the frequency scores of only those subjects who captured on at least five of the six test sessions. Males and females within each age group have been combined. All probabilities are based on one-tailed tests.

AGE GROUP COMPARISONS

TEST BLOCK	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90
1	(13.2)(9.4) 20	(13.2)(7.8) 14	(13.2)(6.2) 9.5 [c]	(9.4)(7.8) 62.5	(9.4)(6.2) 48 [b]	(7.8)(6.2) 72
2	(7.0)(5.8) 23.5	(7.0)(4.0) 13 [a]	(7.0)(2.7) 4 [c]	(5.8)(4.0) 52	(5.0)(2.7) 36 [c]	(4.0)(2.7) 69
3	(3.6)(3.6) 28.5	(3.6)(3.7) 29.5	(3.6)(2.9) 30.5	(3.6)(3.7) 67	(3.6)(2.9) 63	(3.7)(2.9) 74

[a] $p < .05$ [b] $p < .025$ [c] $p < .01$

Table 5.24. Comparison between the different age groups in terms of number of unsuccessful captures on each of the six test sessions. Test sessions have been combined into three successive blocks of two each. Figures in the brackets within each cell indicate the mean number of unsuccessful captures for the two groups being compared and the unbracketed figure indicates their respective U score as determined by the Mann-Whitney U Test. All means and U scores are based on the frequency scores of only those subjects who captured on at least five of the six test sessions. Males and females within each age group have been combined. All probabilities are based on one-tailed tests.

TEST BLOCK	AGE GROUP COMPARISONS					
	30 vs 40	30 vs 50	30 vs 90	40 vs 50	40 vs 90	50 vs 90
1	(5.8) (4.4) 21	(5.8)(2.9) 6 [c]	(5.8) (1.8) 5.5 [c]	(4.4) (2.9) 77.5	(4.4) (1.8) 80	(2.9) (1.8) 64.5
2	(3.6) (2.3) 20.5	(3.6) (2.0) 17 [c]	(3.6) (.4) 3.5 [c]	(2.3) (2.0) 72	(2.3) (.4) 30 [c]	(2.0) (.4) 30.5 [c]
3	(2.2) (1.3) 22.5	(2.2) (1.3) 22	(2.2) (.4) 16.5 [a]	(1.3) (1.3) 73.5	(1.3) (.4) 77	(1.3) (.4) 67.5

[a] $p < .05$ [b] $p < .025$ [c] $p < .01$

between blocks one and two was between the 50 and 90 Day Old groups.

Moreover, comparison between blocks two and three shows that the

30 and 40 Day Old groups nipped significantly fewer times on block

three than on block two; the 50 and 90 Day Old groups, on the other

hand, showed no significant change. Further, no clear-cut pattern

emerged in terms of the number of unsuccessful captures over the

three test blocks (Table 5.20). For example, in the 30 Day Old

group significance existed between blocks one and two but not bet-

ween one and three or two and three. The 40 and 50 Day Old groups

made significantly fewer unsuccessful captures on block three than

on blocks one and two. However, no significance was present between

blocks one and two. In the 90 Day Old group significance was present

between blocks one and two, and one and three, but not between two

and three.

Results of the Mann-Whitney U test analysis indicating signifi-

cant differences between age groups on each test block appear in

Table 5.21 for exploration, Table 5.22 for withdrawal, Table 5.23

for nip and Table 5.24 for unsuccessful capture.

Examination of Table 5.21 shows that no significant difference

existed between the 30, 40, and 50 Day Old groups in terms of the

number of explorations on either test blocks one, two or three.

However, the 90 Day Old group differed significantly from the other

three groups on all three test blocks.

The 90 Day Old group also had significantly fewer withdrawals

than the 30 Day Old group on all blocks, as Table 5.22 indicates.

However, differences between the 40 and 90 Day Old groups and the

50 and 90 Day Old groups were not as marked. For example, signif-

icance between age groups 50 and 90 occurred on both blocks one and

two but not on three. Further, no significance was present between

the 30 and 40, 40 and 50, and 30 and 50 Day Old groups on any test

block except block one where the 30 Day Old group had a significantly

higher frequency than the 50 Day Old group.

Inspection of Table 5.23 shows a similar pattern for the

number of nips per test block. More specifically, both the 30 and

40 Day Old groups differed significantly from the 90 Day Old group

on blocks one and two but not on three. Marginal significance was

also achieved between the 30 and 50 Day Old groups on block two.

Other than this, no significance was present between any group on

any test block.

Lastly, examination of Table 5.24 shows that the 30 and 90

Day Old groups differed significantly from each other on all three

test blocks in terms of the number of unsuccessful captures. Sig-

nificance was also present between age groups 30 and 50 on block

one and between age groups 40 and 90, and 50 and 90, on block two.

This completes the statistical presentation of the main

behavioural measures. Additional less important measures were made

and these will be briefly discussed, for they shed light on the

phenomenon under study. They were the following: the incidence of

capture and carry, the amount of prey eaten, the incidence of pouch

Table 5.25. The number of captors who carried the prey after capture. The capture column indicates the total number of captures made, and the adjacent column (n) indicates the number of subjects within each age group who made that many captures. The next column indicates the number of captors who carried the prey after the first or second capture, third or fourth capture and fifth or sixth capture, respectively. See text for full explanation.

Age Group	Total Number of Captures	n	Number who carried prey after capture	Per cent who carried
30 Day Old	1 - 2	13	6	46%
	3 - 4	11	3	27%
	5 - 6	5	3	60%
40 Day Old	1 - 2	22	4	18%
	3 - 4	19	7	36%
	5 - 6	13	5	38%
50 Day Old	1 - 2	19	2	10%
	3 - 4	17	4	23%
	5 - 6	12	3	25%
90 Day Old	1 - 2	19	2	10%
	3 - 4	16	4	25%
	5 - 6	15	3	20%

after capture, various correlations between capture latency, litter

size and weight of a subject, and last, the exploration and with-

drawal behaviour of the non-captors. Each of these will now be

discussed in turn.

5.2f. Incidence of Capture and Carry

The frequency of carry after the first or second capture,

the third or fourth capture or the fifth and sixth capture appears

in Table 5.25. Results were tabulated from the raw data presented

in Appendix B, Table 6. Table 5.25 shows that out of the 13 subjects

in the 30 Day Old group which made at least one or two captures, six

carried the prey. In other words, 46% of the subjects in the 30 Day

Old group carried the prey after their first or second capture. The

next row for the 30 Day Old group shows that 11 subjects made at least

three or four captures and, of the 11, three carried (the prey) for

an incidence of 27%. Only five subjects in the 30 Day Old group made

as many as five or six captures and, of the five, three carried follow-

ing capture for an incidence of 60%. Therefore, what Table 5.25 shows

is the proportion of subjects who carried the prey following their

first or second, third or fourth, or fifth and sixth captures, respec-

tively.

Further examination shows that in the 40 Day Old group, 18%

of the subjects carried the prey following their first or second

capture, whereas 38% carried following the fifth or sixth capture.

In both the 50 and 90 Day Old groups a greater proportion carried

Table 5.26.   The amount of prey eaten on the initial and final capture for those subjects in each age group who captured on at least two occassions, males and females combined. See text for further explanation.

Age Group	Amount of Locust Eaten	n	
		Initial Capture	Final Capture
30 Day Old (n= 12)	.25	4	0
	.50	5	0
	.75	2	1
	1.00	1	11
40 Day Old (n= 19)	.25	2	1
	.50	5	0
	.75	2	0
	1.00	10	18
50 Day Old (n=18)	.25	1	1
	.50	2	0
	.75	6	0
	1.00	9	17
90 Day Old (n=16)	.25	0	0
	.50	1	0
	.75	0	0
	1.00	15	16

after their fifth or sixth capture than after their first or second.

As mentioned above this same increase also occurred in the 30 and

40 Day Old groups. Further, overall inspection shows that the 30

Day Old captors were more likely to carry the prey than the captors

of the 90 Day Old group. For example, 60% of the subjects in the

30 Day Old group carried following their fifth or sixth capture as

opposed to only a 20% incidence in the 90 Day Old group.

The duration of a bout of carrying varied; often it was very

short; i.e. two to three seconds, while at other times it lasted

for about six to seven seconds. Once a subject stopped carrying

it usually began to eat; rarely did the Experimenter observe a

pouch following carry, and in no instance did a subject begin another

bout of carrying after the first one had ceased. Where a subject

stopped seemed to be random; no marked tendency to bring the prey

back to the nest was observed.

5.2g. Amount of Prey Eaten

In Table 5.26 comparisons are made between the amount of prey

eaten after the initial and final captures for those subjects in

each age group who made at least two captures. Raw data indicating

the amount eaten on each capture appears in Appendix B, Table 7.

In this analysis the session on which a subject made its initial

capture was irrelevant as long as it made one additional capture;

hence comparison between the amount eaten on its first and last could

be made. Thus, for example, for female 10 of the 40 Day Old group

the initial capture occurred on session two (see Appendix B, Table 1)

and following this capture it happened to eat three-quarters of the

locust in the five minutes allowed (see raw data, Appendix A, Table 7).

The final capture for this subject occurred on the last session it

was tested (session 6) and after this capture it ate the locust in

its entirety. So, in summary, on the initial capture this subject

ate three-quarters of the locust while on the final capture it ate

the whole locust. Scores for all subjects were tabulated in this

manner.

Inspection of Table 5.26 shows that nearly every subject in

the four age groups ate the entire locust on the final capture.

This result, however, markedly contrasts with the amount eaten on

the initial capture for the subjects in the 30, 40 and 50 Day Old

age groups. Binomial tests were conducted to determine if signif-

icance existed between the amount eaten after the first capture as

opposed to the amount eaten after the last. Data for the subjects

who ate either 25%, 50% or 75% of the prey were pooled for the pur-

pose of the statistical test. Thus, subjects either ate less than

one or ate one (i.e. the entire locust). Highly significant differ-

ences were obtained for the 30, 40 and 50 Day Old groups (p < .001

for the 30 Day Old group; p < .004 for the 40 Day Old group;

p < .004 for the 50 Day Old group). No significance existed between

the amount eaten on the first and last capture for the subjects of

the 90 Day Old group. This latter result was expected, for as

Table 5.26 indicates, fifteen of the sixteen 90 Day Old subjects

ate the locust in its entirety on the initial capture.

Comparisons between the different age groups in terms of the amount eaten (both the initial and final capture) also yielded significance in a number of cases. The Chi-Square test for independent samples was employed and again data were grouped as to having eaten less than one or exactly one. One-tail tests revealed that the 90 Day Old group ate significantly more than the 30 Day Old group on the initial capture ($x^2 = 17.08$, df = 1, $p < .001$) and likewise ate significantly more than the 40 Day Old group ($x^2 = 5.32$, df = 1, $p < .05$) or 50 Day Old group ($x^2 = 5.84$, df = 1, $p < .02$). Significant differences in the amount eaten on the initial capture also existed between the 30 and 40 Day Old groups ($x^2 = 4.51$, df = 1, $p < .05$) and between the 30 and 50 Day Old groups ($x^2 = 3.90$, df = 1, $p < .05$). Significance between age groups 40 and 50 was not achieved for the initial capture. Further, no significance existed between any of the groups in terms of the amount eaten on the final capture.

The five minute time limit imposed on eating behaviour seemed to be ample time to consume the entire locust if a subject opted to do so. Those subjects who failed to eat the whole locust usually abandoned it before the five minutes had elapsed. In some instances the uneaten locust was deposited on the food pile but in the majority of the cases it was simply left where a subject stopped eating. Subjects, as previously described (Chapter 3, Section 3.3), usually commenced eating from the head down. Uneaten parts which remained were in most cases the thorax, abdomen and legs.

Table 5.27. Number of subjects in each age group who pouched the prey after capture. The six test sessions have been combined into three successive blocks of two each. Only those subjects who captured on at least five of the six test sessions are included in the analysis. Males and females within each age group have been combined. See text for further details.

AGE GROUP	TEST BLOCK	Number who pouched after capture	Per Cent who pouched
30 DAY OLD (n= 5)	1	0	0%
	2	0	0%
	3	0	0%
40 DAY OLD (n= 13)	1	2	15%
	2	5	38%
	3	7	53%
50 DAY OLD (n= 12)	1	1	8%
	2	4	33%
	3	3	25%
90 DAY OLD (n= 15)	1	3	20%
	2	7	46%
	3	6	40%

Correlations were also taken to determine if a relationship

existed between the culumative latency to capture and the amount

eaten on the initial capture. Results of the non-parametric Spearman

Rank correlation test yielded the following coefficients; r_s = -.006

for the 30 Day Old group; r_s = .31 for the 40 Day Old group;

r_3 = .40 for the 50 Day Old group. These coefficients failed to

reach significance at the .05 level (two-tail tests). No correla-

tion was taken for the 90 Day Old group because of the lack of

variability in terms of the amount eaten (i.e. all subjects with

the exception of one ate the entire locust on the initial capture).

5.2h.   Incidence of Pouch after Capture

Raw data indicating the incidence of pouch after capture

appears in Appendix B, Table 8. The frequency of this behaviour

for those subjects in each group who captured on at least five of

the six test sessions is presented in Table 5.27. Test sessions

in Table 5.27 have been blocked and the males and females combined.

Exclusion of the non-captors from this analysis was justified

because no subject which made fewer than five captures ever pouched

the prey, with the exception of one male in the 30 Day Old group.

Inspection of Table 5.27 shows a clear increase in the incidence

of pouching over the successive test blocks for the subjects in

the 40, 50 and 90 Day Old groups. More than three times as many

subjects in the 40 and 50 Day Old groups pouched on block three than

on block one and the increase from block one to block three for the

90 Day Old subjects was twofold.

Table 5.28. Correlations coefficients between
capture latency and weaning weight (W.W.),
capture latency and capture weight (C.W.), and
capture latency and litter size (L.S.) as
determined by the Spearman Rank Correlation
Test.

AGE GROUP	W.W.	C.W.	L.S.
30 DAY OLD	-.11	-.53[a]	-.001
40 DAY OLD	.06	.28	.30
50 DAY OLD	-.12	-.04	-.33
90 DAY OLD	-.26	-.25	-.12

[a] p < .02

5.2i.   Relationship between Capture Latency, Litter Size,

Weaning Weight and Capture Weight

Spearman Rank correlation coefficients, corrected for ties,

were computed in order to determine if a subject's litter size,

weaning weight (i.e. weight at 23 - 25 days) or capture weight

(i.e. weight following the last test) varied systematically with

its latency to capture. The raw data from which the computations

were made are presented in Appendix B, Table 9 and the coefficients

appear in Table 5.28. Latencies in this analysis consisted of the

subject's cumulative total for the six test sessions. Inspection

of Table 5.28 shows that the only significant correlation achieved

was a negative one, between capture weight and capture latency for

the subjects in the 30 Day Old group (t = 2.75, df = 21, p < .02,

two-tail test). More specifically, the heavier subjects in the 30

Day Old group captured with a significantly shorter latency.

The litter sizes from which the subjects were derived ranged

between two and thirteen, and the mean weaning weights and capture

weights for the subjects in each age group were as follows: 27 and

47 g. for the 30 Day Old group; 30 g. and 58 g. for the 40 Day Old

group; 30 g. and 66 g. for the 50 Day Old group and 29 g. and 84 g.

for the subjects of the 90 Day Old group.

5.2j.   Behaviour of the Non-Captors

In most of the analyses presented thus far data of the non-captors

219.

has been kept separate from that of the captors. This was done

primarily so that the effects of repeated testing on the various

behaviours would be most clearly shown and, in addition, to provide

a more representative picture of the way in which a captor's behav-

iour changed with experience.

Several features, however, characterized the behaviour of the

non-captors. First, they rarely nipped or attempted capture; hence,

meaningful presentation of this data could not be made. Second,

when they did explore, their explorations tended to be of short

duration (usually about 1 - 3 seconds) and further the number of

explorations did not decrease with repeated testing as it did with

the captors. Inspection of the exploration data for the 20 subjects

in this experiment (age groups combined) who failed to make a single

capture showed that they made, on average, 18.3 explorations on block

one, 15.3 on block two and 14.9 on block three. Third, unlike the

captors, their withdrawal behaviour tended to remain at relatively

high rates on all three test blocks. On block one, for example, the

non-captors had on average 7.9 withdrawals; on block two there was

an average of 6.7 and on the last block an average of 4.3 withdrawals.

Non-captors who showed no withdrawal following exploration usually

behaved in an indifferent manner; i.e. cage exploration or digging.

5.3. DISCUSSION

The empirical results generated from this study are concordant

with the qualitative observations made in the pilot study. In

general, the most important results showed:

1) an increase in the likelihood of capture with repeated

   exposures to the prey;

2) a decrease in latency to capture with successive

   captures;

3) a concomitant decrease in the frequency of behaviours

   which aid in capture.

Moreover, this first experiment demonstrated that the age

of a hamster was a significant factor in determining the likelihood

of capture, as well as the relative importance of the effects of

experience. In short, it was found that both the variables of age

and experience played important roles in the development of locust

capture by hamsters.

Some elaboration is necessary if these findings are to be

more fully understood. Specifically, the word experience as it

is used in the present context is nebulous and summary; hence,

a more precise meaning needs to be offered. First, one could take

it to mean the mere exposure to the prey as stated in point one

above. Repeated exposures, as the results showed, led to an increase

in the incidence of capture. That is to say, significantly more

subjects in age groups 30, 40 and 50 captured on blocks two and

three than on block one as Figure 5.2 and Table 5.3 clearly indicate.

Now this type of experience in the form of repeated exposures

as it is referred to here means no more than the repeated experience

of sensory contact with the prey. This occurred in the present exper-

iment once every two days for a period of five minutes for those

subjects who failed to capture on any particular session. One can

appreciate the importance of this type of experience by scrutinizing

the behaviour typical of the younger hamsters during their initial

encounters with the prey. During the initial phases relatively

few attempted capture (i.e. by nipping, seizing and grasping);

instead, the behaviour of most was characterized by exploration and

withdrawal. Such behaviour was, in nearly every case, antecedent

to the first nip or attempted capture and the persistence of it

depended mainly on the age of the hamster. For example, subjects

in the 90 Day Old group, on average, behaved in this ambivalent

manner for perhaps two or three minutes into the first test session

before they nipped or attempted capture. On the other hand, for most

of the subjects in the younger age groups, such behaviour in the

majority of cases continued well into the second and third test

sessions before capture was attempted. The picture which emerges

then is that during the first few minutes of the initial test session

(for most of the 90 Day Old subjects) or perhaps even during the

entire initial session and into the second and third (for the majority

of subjects in the 30, 40 and 50 Day Old groups) experience in the

form of exposure to the prey took place without accompanying attempts

at capture. One must ask, then, what function, if any, did this type

of experience serve?

As stated above, the effect it had was to increase the likelihood

of capture on subsequent tests. As to its function, though, it would be very plausible to argue, in light of the decrease in frequency and intensity of withdrawal behaviour with successive tests, that the initial exposures served to habituate the fear a hamster had for the unfamiliar locust. That novelty can induce an unconditioned fear response in the naive animal is well known and documented in the psychological literature (reviews can be found in Bronson, 1968, or Gray, 1971) and it is likely that this factor was operating in the situation we are discussing here. Consequently, through the process of habituation a naive hamster probably lost its fear of the locust and hence was in a better position, motivationally at least, to attempt capture on the later test sessions. This, then, was the function of the first type of experience as discussed.

Thus having learnt not to fear the locust, experience of a second kind, for some, took hold; namely, learning to perfect the prey-capture techniques. At first, as described in Chapter 3, the attempts at capture were often unsuccessful. The initial·nips occasionally missed their mark by as much as half-inch and the number of explorations and withdrawals occurred at a relatively high rate. However, after experiencing several successful captures, nips came to be aimed at a different place (exclusively towards the anterior end) and the hamster started grasping the prey more anteriorly. This overall increase in efficiency was further reflected in the decreased latency to capture with successive captures (see Figure 5.5). In short, after the experience of several successful

captures, a hamster needed fewer nips to make capture, made fewer

explorations and unsuccessful captures prior to capture and captured

with a significantly shorter latency. For lack of a better term this

second type of experience may be functionally labelled 'practice'.

Up to the point of actually making capture, then, there seem

to be two principal types of experience involved; namely, the

experience of exposure and the experience of practice. To make

matters even more complex it seems possible to identify yet another

qualitatively different type of experience; this is the experience

of eating the locust. Obviously this differs from the other two

experiences in that it occurs after the capture has been made.

What effect eating the locust has on the rest of the behaviours

in the predatory sequence is a theoretical point of considerable

interest, and one to which we will shortly turn our attention.

However, before we speculate what effect this act might have we

should recognize that the captors of the younger age groups usually

did not eat the locust in its entirety at first (see Table 5.26).

It was usually only after experiencing one capture (plus partial

eat) that they came to eat the whole locust on a subsequent capture.

Thus again we have another behaviour within the predatory sequence

that changes with experience. Knowing this, two questions present

themselves; namely, one, why was more of the locust consumed on the

second and subsequent captures and two, even more fundamentally, why

did the captors come to eat the locust at all?

In regard to the latter several explanations can be offered, the most parsimoneous of which suggests that hamsters, as omnivores, possess a disposition to treat any novel palatable substance as food. This explanation is feasible in light of the wide range of edible novel substances that laboratory hamsters are known to feed upon; such a list might include sunflower seeds, cheese, carrots, grass, wheat kernels, chocolate, fresh fruit and dried milk. Most of these novel foods when first offered to a naive hamster (i.e. one who has never eaten them before) are treated in basically the same way; i.e. exploration of it, followed by a brief taste followed by eat (author's personal observations).

What is being suggested then is that the locust is treated as food simply because it is palatable and novel (having earlier lost its fear-provoking properties through the process of habituation). The novelty hypothesis gains support from some research that has been done with the domestic rat. Several authors have found that rats exhibit a strong neophilia for novel food substances as opposed to familiar ones when given the choice between them (Bronson, 1966; Welker and King, 1962). Hamsters in the present experiment were confronted with basically the same situation; i.e. novel locust as opposed to the familiar lab chow.

The second explanation assumes that the feeding response and the capture response are all part of the same motivational system; hence, the animals that possess the motivation to capture also auto-matically possess the motivation to eat what they captured - i.e. the

locust. For this reason eating should sequentially come to follow

capture with very little delay. The findings of this experiment

support this theory; in nearly every case a hamster did eat some

of the locust immediately after capture.

Last, one could argue that a hamster eats the locust because

it has a specific hunger for it. This assertion is essentially

correct if one accepts a specific hunger as being the "tendency of

an animal to ingest certain food stuffs when given a choice, whether

or not it coincides with any known nutritional deficiency" (Balgagura,

1973, p-133). On the other hand, if specific hungers are to be talked

about only when a specific need arises for a specific nutritive sub-

stance, as it traditionally is, then hamsters in the present experi-

ment probably had no specific hunger for locusts. It is known from

the excellent research of Rozin and colleagues (see Rozin and Kalat,

1970 for a critical review) that specific needs usually give rise to

characteristic symptoms when a specific nutritive substance is with-

held. In the domestic rat, for example, thiamin (vitamin B_1)

deficiency is characterized by weight loss, anorexia, paleophobia

for familiar foods and hypothermia. If hamsters in the present

experiment were in need of some essential vitamin or mineral contained

in the locust (perhaps protein) then one would expect this deficiency

to be reflected in some behavioural (perhaps anorexia) or physical

symptom (perhaps weight loss). However, both of these reactions

which occur in thiamin deficient rats did not occur in the hamsters,

nor did any other symptom appear suggestive of any type of specific

hunger. Hamsters in the present experiment continued to eat their

lab chow (which contains a surfeit of the necessary vitamins and min-

erals necessary for normal body growth and maintenance) and further

casual observation suggested that all were in a relatively 'healthy'

state. Thus, in short, the explanation of a specific hunger for

locust eating would seem to carry little weight.

We must now return to the other question posed above; namely,

why the subjects in the younger age groups ate more of the locust

after the final capture. The most reasonable explanation for this

suggests that after the initial capture some ambivalence towards the

locust still existed; hence, still being a relatively novel object

this palatable food substance (i.e. the locust) was abandoned rather

than consumed. However, concomitant with this existing state of

ambivalence a hamster also probably developed a specific appetite

for it due to having tasted it, as well as through partial consump-

tion. This seems likely in the light of the cogent arguments put

forth by the eminent P.T.Young (see Young, 1948, 1967). Young avers

that in the establishment of an appetite for a particular food sub-

stance palatability is one important factor that must be considered.

Young in his writings uses the term palatability to mean the "immediate

affective reaction (liking or disliking) of an organism which occurs

when a food stimulus comes in contact with the head receptors" (1948,

p-320). Now by the very nature of the prey-catching act on the

part of the hamster (seizure with the mouth and grasp with the fore-

paws) the food stimulus, in this case the locust, is brought into

direct sensory contact with the head receptors (i.e. the visual,

olfactory, tactile and gustatory senses). The immediate affective

reaction, to use Young's term, is no doubt one of liking, for after

the initial capture hamsters in the present experiment carried on
to eat at least part of the locust; never did they show any
behaviour indiciating that the locust was noxious or distasteful.
Consequently, through the initial act of capture and through the
partial eat which followed, a hamster probably learnt that the locust
was both a palatable and edible food substance. However, during the
initial phases of the interaction the ambivalence which a hamster
still had towards the locust probably prevented total consumption
within the time allowed (five minutes). After several captures,
though, this learnt appetite probably became more deeply entrenched
and coupled with the waning of ambivalence (both to live and captured
prey) it thus came to eat the locust in its entirety. In short, a
hamster learnt that the locust was a potential source of novel food
and this is the reason why later captures were followed by total con-
sumption. It follows then that the eating of locusts by hamsters
following capture should be classified as a learnt appetite (see
Scott and Quint, 1946 for a classifactory scheme of feeding habits).

Further, the increased efficiency in making capture which was
observed in this experiment may also be attributed, in part, to the
experience of prey feeding. That is to say, such improvement could
possibly be explained in terms of a principle which has long been the
cornerstone of behaviouristic thought. Formally stated, it is what
E.L.Thorndike (1911) termed the <u>law of effect</u> and one hardly needs to
say that it has been one of the most fundamental explanations put
forth by scientists to explain certain behavioural phenomena. Knowing
this, one might hypothesize that the instrumental behaviours involved

in prey capture were 'shaped-up' and reinforced (much in the same way

a rat learns to press a bar) by the event which followed their occur-

rence and that this subsequent event, eating the prey, was positive

and hence potentially reinforcing cannot be disputed, for once a

hamster learnt what it was it came to eat more of it. Hence, in

accord with Thorndike's principle the results of this first experi-

ment might be suggestive of the fact that eating the locust after

capture was reinforcing; this in turn permitted development of the

behaviours needed for capture.

According to a second theory, and one which seems more plausible,

the act of capture is a species-typical behaviour. Therefore, the

basic behaviours needed when they do come forth (which in large part

is determined by experiential factors)   will be self-reinforcing

in their own right but, at first, somewhat crude. Reinforcement in

in the conventional sense (eating the locust) is not needed to 'stamp

in' the behaviours, as implied above, but may be needed to some degree

for their refinement and perfection.[3]

Thus the fact that a hamster became a more efficient and skilled

captor with experience is not all that surprising. What is even more

difficult to understand, though, is why a hamster even attempted to

capture in the first place. That is, why after its fear of the locust

had habituated did it come to nip at, seize and attempt to grasp the

prey with the forepaws? Further, why were there such great individual

---

3.. In Chapter 8 it will be argued that eating after capture in
   large part strengthens the tendency to capture.

differences between subjects within the same treatment group? Considering the explanations put forth by other psychologists and ethologists studying the predatory behaviour of other mammals, such as rats and cats (see Chapter 2, Section 2.4b.4), and in accord with the second explanation offered above, it would be reasonable to assume that all hamsters have within them a propensity, a predisposition or some potential to capture small moving objects like locusts. And what is even more important to realize is that when this potential is manifested a hamster has within its behavioural repertoire a very specific set of responses (which at first are crude and unrefined) to deal with the situation in the most biologically appropriate way (i.e. capturing the locust). The word specific is used for two reasons. One, because of the nipping and seizing behaviour which is so obviously well suited to maim and capture small prey-like objects and, two, because of the co-ordination between the nipping, seizing and grasping behaviours. The nipping and seizing behaviours must have evolved specifically as a food-getting or prey-capture technique; rarely have they been observed to occur in any other behavioural context. The fact that an experienced hamster captor grasps the locust to feed on it is not unusual because all hamsters - and for that matter most species of the order Rodentia - feed on other food substances in essentially the same manner. What is remarkable, though, is that the naive hamster grasps the prey immediately after seizing it in the mouth in a co-ordinated fashion from the onset and well before it had ample enough time to learn that it was in fact an edible food substance. So in essence, what I am suggesting is that all hamsters come equipped with a propensity, a specific set of behaviours (nipping and seizing) and an unlearned co-ordinated sequence between behaviours in order to effectively treat small prey, like locusts, as food.

If such a propensity exists then it would be feasible to argue that some individuals possess more of it than others. This in turn could explain the great individual differences in the tendency to capture. This difference in propensity could arise from two sources; either from one, the differing experiences an individual underwent prior to the initial capture or, two, the genetic makeup or genotype of the individual. In the present experiment more weight must be attributed to the latter, for essentially this was the only factor that was allowed to vary among the individuals within the same treatment group. To ascribe individual differences in prey-capture to differences in genotype would seem tenable for this explanation has been used in the past to explain individual differences in other types of hamster behaviour (Lawlor, 1960).

The last matter we must deal with before moving on to the next chapter is the age difference in locust capture. This perhaps was the most salient finding of the first experiment. Older hamsters not only showed a greater likelihood of capture but also captured with a shorter latency and also after fewer explorations, withdrawals, nips and unsuccessful captures. Further, when compared to the 30 Day Old subjects the 90 Day Old subjects ate more of the prey after their first capture, showed a greater incidence of pouching the prey and were less likely to carry the prey. Indubitably, then, these results suggest that in addition to experience, age is an important factor in not only determining the likelihood of capture but also the efficiency in which a capture is made. Why the age of a hamster should have such a strong influence on prey-capture could stem from the following possibilities: either one, the brain structures which

control hamster predatory behaviour have not yet developed in the

younger animals; two, some hormone must be present which the older

animals have and the younger animals lack and, three, older animals

are physically larger and thus consequently less easily intimidated

by the novel locust. The relevance of hormones will be considered

in the next chapter and that of subject size will be discussed in

Chapter 12.

6

THE EMERGENCE OF THE BEHAVIOUR

Results from the first experiment showed that the incidence

of capture was approximately 25% for the subjects from the 30 Day

Old group. In this experiment the earliest age a hamster was tested

was at 30 days. Therefore, it became desirable to know if hamsters

younger than 30 days would capture. Hence, the experiment reported

below set out to determine how old a hamster had to be before it

could capture successfully.

6.1.   DESIGN AND PROCEDURE

The subjects were 48 hamsters derived from nine litters born

between 1st December and 4th December, 1971. All were weaned at 19

days of age, housed individually in a testing compartment and random-

ly assigned to one of the following test groups: 20 - 21 days;

22 - 23 days;   24 - 25 days;   26 - 27 days and 28 - 29 days. The

test for locust capture was administered only once and this occurred

when a subject reached the age corresponding to the group to which

it was assigned.

The test consisted of introducing a 4th instar locust nymph into a subject's compartment and leaving it there for a maximum of 24 hours. Following the introduction, subjects were observed continuously for approximately 15 minutes; if no capture occurred within this time their compartments were subsequently checked periodically throughout most of the 24 hours which followed for signs of a capture having been made. If a capture was not observed directly, then it was assumed to have occurred if the locust was missing from the compartment (the hamster having eaten it) or if parts of its body were on the cage floor (i.e. legs, abdomen, etc.). The approximate latency to capture was then noted. If a subject failed to capture within 24 hours the locust was removed and the test terminated. Subjects during the entire course of the experiment had *ad lib* access to food and water. Further, to prevent the locust from hopping out of a compartment during the course of a test, the two holes in the compartment top were covered with sellotape.

6.2.   RESULTS

Nine of the 48 subjects assigned to the five experimental groups died prior to testing. Of the nine who died three were from the age group to be tested at 20 - 21 days, one was from the 22 - 23 Day Old group, two were from the 26 - 27 Day Old group and three were from the age group whose test commenced at 28 - 29 days. Raw latencies to capture for the remaining 39 subjects appear in Appendix B, Table 10. In terms of the percentage who captured, the results show an 80% (4 out of 5) incidence for the subjects tested at either 20 - 21

days, a 90% (9 out of 10) incidence for the 22 - 23 Day Old group

and a 70% (7 out of 10), 100% (9 out of 9) and 100%(5 out of 5) incid-

ence for the subjects tested at either 24 - 25, 26 - 27, or 28 - 29

days of age, respectively. Latency scores ranged from three minutes

to approximately eight hours.

6.3.   DISCUSSION

Two important findings emerge from this study. First, it should

be noted that nearly all subjects when given an uninterrupted 24

hours in which to make capture, did in fact capture. This result,

in turn, could explain the relatively low incidence of capture by

the younger hamsters in the first experiment. It may be recalled

that hamsters in the initial study were given six interrupted sessions

of five minutes each (for a cumulative time of 30 minutes). In terms

of cumulative time, then, this was far less than the total time

allowed the subjects in the present experiment. Comparing the over-

all incidence of capture by the hamsters in each of these experiments

thus suggests that either the length of a test session or 'the cumula-

tive total time of the sessions combined were artifacts of the experi-

mental situation influencing the likelihood of capture.

This prolonged 24 hour forced exposure to the prey (remember

hamsters had no way to escape) probably acted on the first type of

experience as discussed in the previous experiment. It was argued

that through the experience of exposure a hamster learnt not to fear

the locust, and it may be remembered that this was one stage in the

experiential process a hamster passed through before attempting

capture. This lengthy exposure of 24 hours as it occurred in the

present experiment was in all likelihood ample time (in fact prob-

ably more than enough) to allow a hamster's fear response to adequately

habituate and so consequently, as a result, nearly all hamsters came

to behave in the manner typical of their species - i.e. by capturing

the locust.

The other important finding of this experiment showed that

hamsters as young as 20 days would capture. This finding thus

suggests that locust capture has no direct hormonal basis. The

sexual hormones, testosterone and estrogen, critical in the main-

tenance and initiation of several other hamster behaviours (consult

Chapter 3 for references) do not begin to circulate in quantity until

approximately 40 days of age. Thus, if these hormones were essential

for the development of prey - capture then one would not expect to

find too many hamsters capturing before 40 days of age. However, as

we have seen in this experiment, hamsters captured at 20 days of age

and in the experiment prior to this at 30 days of age. Further, the

belief that hormones have a negligible effect on prey-capture is

buttressed by the finding of no sex difference in this behaviour

(see Experiment 1, Figure 5.1). Because of these findings we may

dismiss the view that the age difference in locust capture, as repor-

ted in Experiment 1, was due to the presence or absence of the sexual

hormones.

Although this experiment was noteworthy it still left open the

question of when exactly the behaviour 'emerges'. In light of
the present findings it would be judicious to render a guess at
about 13 to 16 days, for this is the age when a hamster first
begins to get fairly mobile (Campbell and Mabry, 1972) and,
further, this is the age when its eyes first open (Dieterlen,
1959).

7

THE FREQUENCY OF PREY PRESENTATION

Besides the length of a test session another artifact of the first experiment which might have influenced the probability of capture was that of the frequency of prey presentation. The reader should note that the procedure in the first experiment (Chapter 5) consisted of presenting the prey to a subject once every other day. With this inter-trial interval (abbreviated ITI) of two days, latencies to capture for the majority of subjects decreased significantly in a linear fashion. This being the case, one could well argue that the decrease, in part, could have been due to the relatively short two day ITI. Therefore, one could justly ask if locust capture would develop in a similar manner if subjects were presented prey, say, once every five days or perhaps once every ten days. If our argument holds - that is, that locust capture is, to an extent, a learnt phenomenon constructed upon certain basic predispositions - then one would expect the ITI to have some influence. Learning studies in the past, with both humans and animals, have shown that the spacing of trials has a strong influence on the acquisition of certain learnt behaviours (Deese and Hulse, 1967; McGaugh, Jennings and Thompson, 1962; Wimer, Symington, Farmer and Schwartzkroin, 1968). Thus, in essence, the question for us is one of massed versus

spaced presentations, and whether or not this factor has an effect

on the acquisition of locust capture is what this experiment set out

to determine.

7.1.   DESIGN AND PROCEDURE

The subjects were 42 hamsters derived from seven litters born

between 1st January and 1st March, 1972. Subjects were weaned at

24 or 25 days of age, placed in an individual compartment and ran-

domly assigned to one of three experimental groups. Subjects in

the first group, ITI-1, had a 4th instar locust introduced into their

compartment for a five minute test on four successive days. Subjects

in the second (ITI-5) group and third (ITI-10) group were likewise

tested, in total, on four occasions; however the interval between

each test differed. Subjects in Group ITI-10 were initially tested

at 30 days of age and subsequently on days 40, 50 and 60; hence the

10 day ITI. Testing for the subjects in Group ITI-5 commenced at

either 30, 35, 40 or 45 days of age and continued on the following

days: days 35, 40 and 45 for the subjects initially tested at 35

days; days 45, 50 and 55 for the subjects initially tested at 40

days; days 50, 55 and 60 for the subjects initially tested at 45

days. Subjects in Group ITI-1 were initially tested at either 30,

40, 50 or 60 days of age and subsequently on the three days immedi-

ately following, irrespective of the age when first tested. Thus

subjects in this group were tested once daily between the following

ages: 30 - 33 days; 40 - 43 days; 50 - 53 days and lastly 60 - 63

days.[1]

---

1.   Counterbalancing the age of test onset in Groups ITI-1 and ITI-5
     was necessary in order to neutralize the potentially confounding
     factor of age.
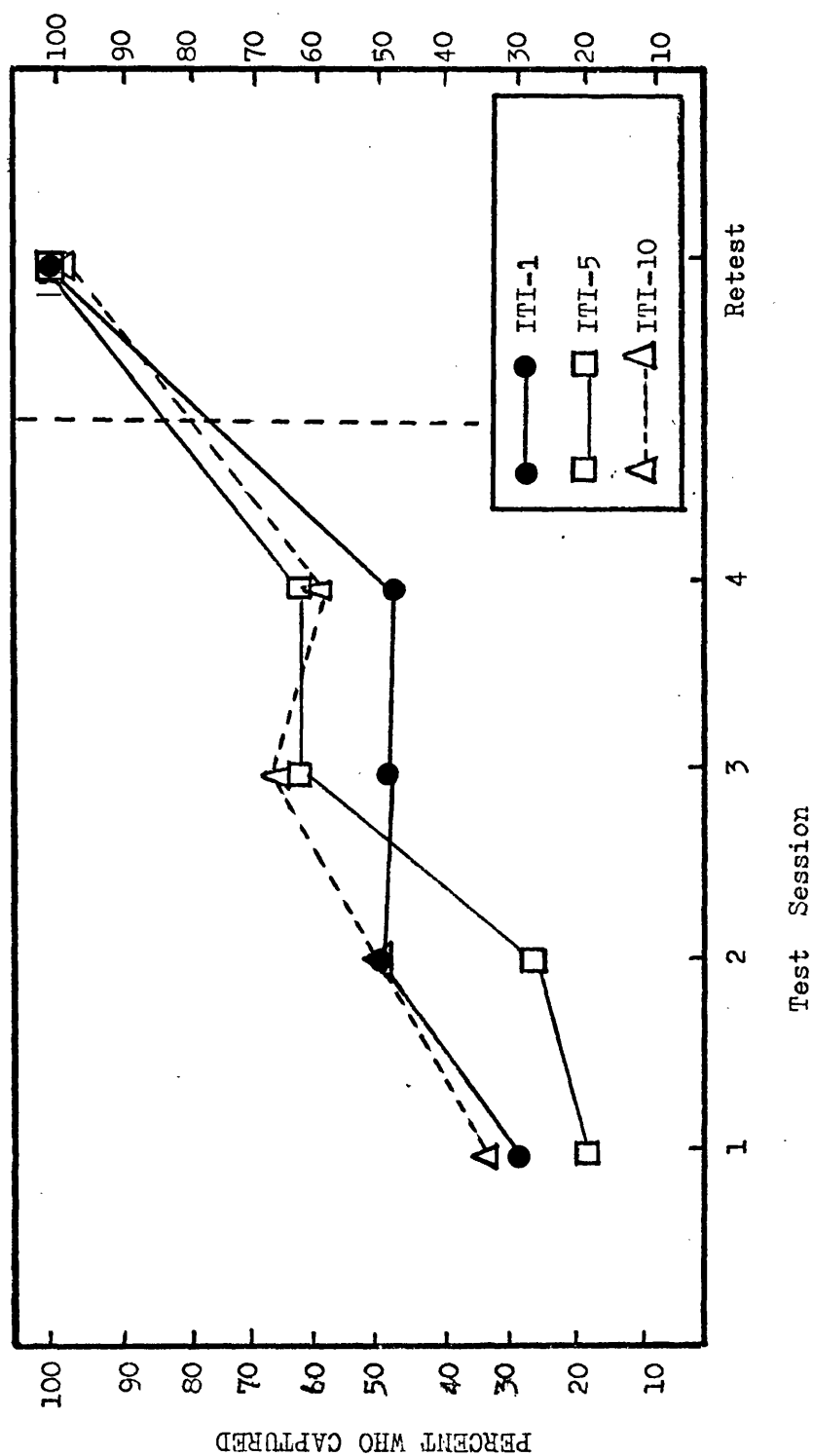
Figure 7.1 Percentage of captors in each group on the first four tests and on the retest. Males and females within each group have been combined.

Approximately 70 days following their last test all subjects

were again tested with a 4th instar locust for a maximum of five

minutes. The principal measure taken during the four tests and the

re-test was latency to capture and this was recorded on a stop

watch. Subjects during the entire course of the experiment had

ad lib access to food and water.

7.2. RESULTS

Nine of the 42 subjects died before the completion of the

initial four tests. These included four subjects from ITI-1

(M1, M3, F4, F7), three subjects from ITI-5 (M3, M6, F6) and two

subjects from ITI-10 (M1, M7). Another subject from ITI-10 (M6)

died in the interval between the last test and re-test. Data

obtained from this subject for the first four tests was included

in the statistical analysis reported below.

Raw latencies to capture for the subjects in each group

appear in Appendix B, Table 11. Those subjects who failed to

capture on any test were assigned the maximum score of 300 seconds.

Looking first at the proportion of captors in each group,

one notes a general increase in the number who captured over the

four test sessions. This trend upward is illustrated graphically

in Figure 7.1. Analysis of this data with a Cochran Q-test revealed

that significance existed between the test sessions in groups

ITI-5 (Q = 14.64, df = 3, p < .01) and ITI-10 (Q = 8.07, df = 3,
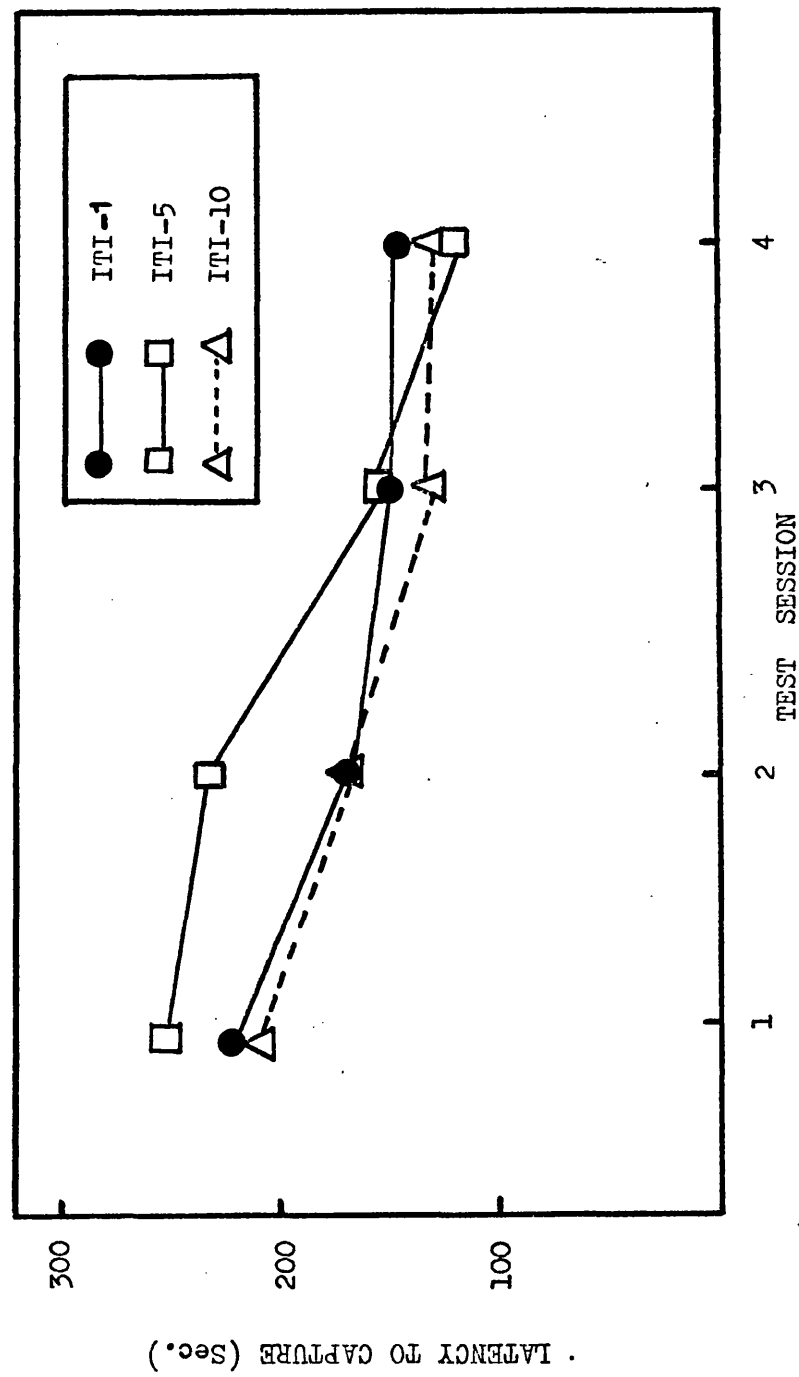
Figure 7.2. Mean delay between presentation and capture of a locust for all subjects in Experiment 3. Males and females within each group have been combined.

242.
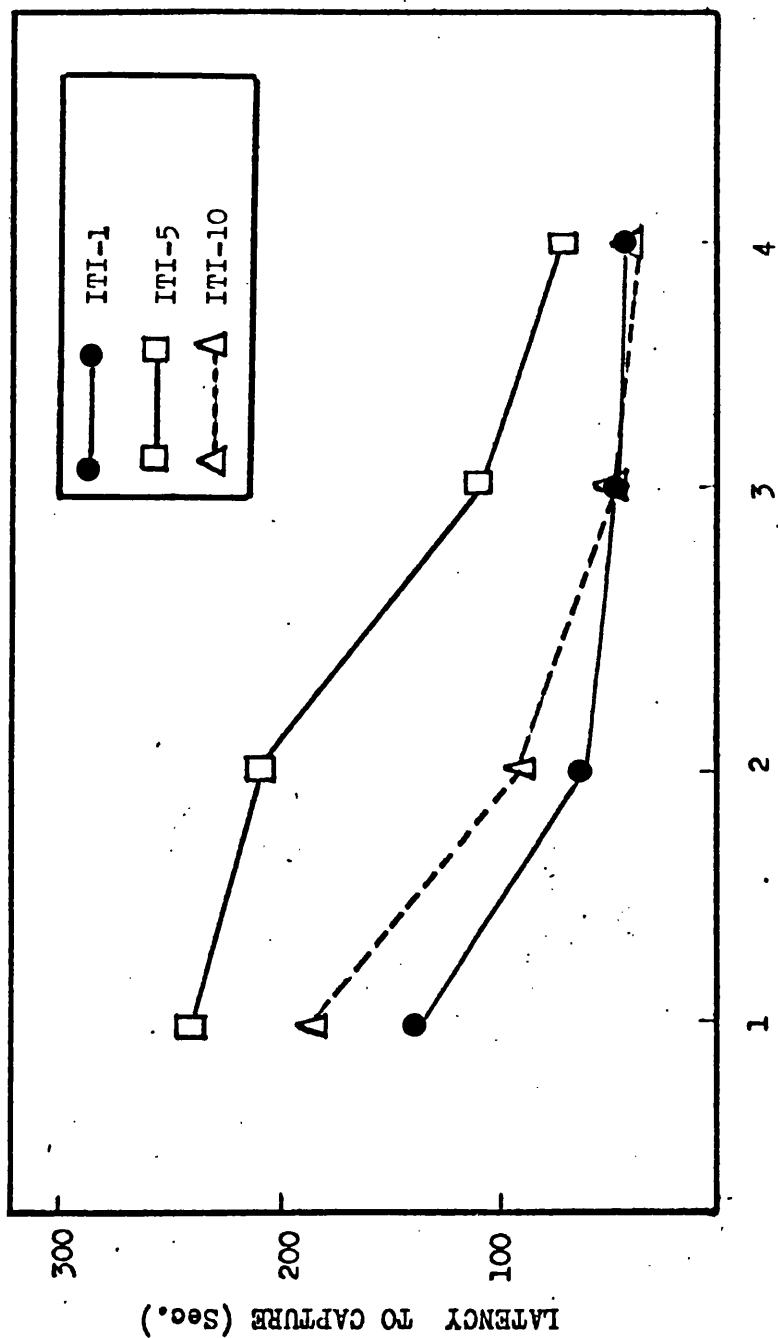
Figure 7.3. Mean delay between presentation and capture of a locust for those subjects in Experiment 3 who captured on at least one occasion Males and females within each group have been combined.

p $<$ = .05). No significance was achieved in group ITI-1 (Q = 6.0,

df = 3, p $<$ .20). Further examination of Figure 7.1 shows that

100% of the subjects in all three groups captured on the re-test.

Chi-square tests were then conducted to determine if signifi-

cance existed between groups in terms of the proportion of captors

on any test block. Results showed that the three groups did not

differ significantly from each other on any test session. On

session two (see Figure 7.1), where the largest differences occur-

red, actual significance was not achieved (X^2 = 4.5, df = 1, p $>$ .50

for groups ITI-1 vs. ITI-5; X^2 = .47, df = 1, p $>$ .30 for groups

ITI-5 vs. ITI-10).

In Figures 7.2 and 7.3 the mean latencies are presented.

Figure 7.2 differs from Figure 7.3 in that in the former the means

are based on the latencies of all subjects (males and females com-

bined) whereas in the latter the means were derived from the scores

of only those subjects who captured at least once (i.e. non-captors

excluded and males and females combined). A Friedman two way

analysis of variance was applied to the data of Figure 7.2 and the

results revealed a lack of significance between test sessions for

Group ITI-1 (X_r^2 = 3.3, df = 3, p $<$ .50, two-tail test); however,

significance was achieved for groups ITI-5 (X_r^2 = 9.72, df = 3,

p $<$ .05, two tail test) and ITI-10 (X_r^2 = 16.10, df = 3, p $<$ .01,

two tail test).

Latency scores of the captors only (Figure 7.3) were analysed

by the Friedman test and the results also showed a lack of significance

between the four test sessions for Group ITI-1 (X_r^2 = 6.84, df = 3,

p $<$ .10, two tail test); however, significance was achieved in groups

ITI-5 (X_r^2 = 13.61, df = 3, p $<$ .01, two tail test) and ITI-10

(X_r^2 = 15.07, df = 3, p $<$ .01, two tail test).

The data in Figure 7.2 was also analysed by the Mann-Whitney U

test in order to determine if the groups differed significantly from

each other on any test sessions. The results obtained were entirely

negative.

7.3. DISCUSSION

The results of this experiment, although not as clear cut as

one might hope, are still suggestive of the fact that the interval

at which the prey is presented has some influence on the development

of locust capture. For example, naive hamsters presented prey once

a day for four consecutive days showed no significant decrease in

latency to capture (Figures 7.2 and 7.3); moreover, there was no

significant increase in the actual number who captured (Figure 7.1).

On the other hand, subjects which experienced prey presentation once

every five days, or once every ten days, did exhibit a significant

decrease in latency and, further, the number who captured also inc-

reased significantly. Thus, in light of these findings and the

findings of Experiment 1 (where the ITI was two days) it appears that

if repeated tests of a fixed duration (five minutes) are given, then

an ITI of at least two days is necessary for the optimal development

of locust capture. That is to say, if latencies are to significantly decrease and the proportion of captors significantly increase with repeated testing, then subjects must be presented prey with no less than 48 hours between successive presentations.

This conclusion, however, must remain tenuous for two reasons. First, the latency data for the captors of Group ITI-1 (Figure 7.3) nearly reached significance ($p <$ .10). It may well have been that if they were given a total of six tests rather than four (as in Experiment 1) then significance between test sessions would have eventually been achieved.

Second, no significance was found between groups on any test session either in terms of latency to capture or the proportion of captors. If the effect of the ITI was of a sizable magnitude then one would have expected significance to manifest itself in either one of these measures; however, as Figure 7.2 and Figure 7.3 indicate this was clearly not the case.

Aside from the marginal effects of the ITI the other major finding of this experiment was that 100% of the subjects captured when re-tested 70 days after their last test. Thus this finding buttresses the belief that age is a variable of paramount importance in determining the likelihood of capture. The fact that non-captors from each ITI group captured on the re-test (after the initial failure to capture on the initial series of tests) must in large part be attributed to age (subjects ranged between 104 - 134 days)

and also in part to their earlier exposures to the prey.

The fact that 100% captured on the re-test is further indicative of the stability of the behaviour. It may be recalled that in addition to the non-captors which captured for the first time on the re-test there were subjects which had previously captured on the initial four tests. For these latter subjects, then, there was at least 70 days interval between capture on the re-test and their previous capture. Further, the stability of prey capture was reflected in the fact that very few reversals of the reaction occurred. That is to say, in this experiment, as well as in Experiment 1, once a subject made capture it continued to capture in a reliable fashion whenever tested.

Thus it can be argued that the development of locust capture can be significantly affected by certain experimental artifacts. Taken together, Experiment 1 (Chapter 5) and Experiment 2 (Chapter 6) showed one such factor to be the length of a test session, and in the experiment reported in this Chapter the interval between prey presentation was found to play a small but significant role.

Hence, having dealt with the two most obvious methodological features of the basic experimental design we will now re-direct our attention to the actual behaviour itself, and scrutinize more closely the role the different experiential components play in the development of the predatory response. One such component, which was briefly discussed in Chapter 5, was that of eating (the prey) after capture. The effect of this experience will be the topic of concern in the next chapter.

8

THE NATURE OF THE EXPERIENCE

It has been emphasized in previous chapters that a hamster's
experience with the prey plays a paramount role in the development
of the predatory response. Further, it may be recalled from the
discussion in Chapter 5 that three principal types of experience
could be identified. To recapitulate, these included the experience
of exposure, the experience of capture and the experience of eating
that which was captured, the prey.

Thus, having identified the three major types of experience
involved in the development of this behaviour, it seems worthwhile
to take the analysis one step further in order to determine the
relative influence of each. In this chapter, then, and in the two
chapters which follow, experiments will be reported which attempted
to separate each of these three kinds of experience.

For convenience now, and for reasons that should later become
apparent, these three kinds of experience will be dichotomized into
two main categories. The first includes both the experience of
exposure and the experience of capture and collectively these will
be referred to as the pre-capture experience. Therefore, behaviours
like prey exploration, nip at the prey, withdrawal from the prey and
any attempted capture that was unsuccessful will be labelled pre-

capture, for it is these kinds of experience a hamster undergoes

before it actually makes capture. Subsequently, the second type

of experience, and one which invariably occurs if a hamster is

successful in making capture, is that of eating the prey, and this

will be separately categorized as the post-capture experience.

The problem for us then, at this stage, becomes one of det-

ermining the relative importance of each of these two main cate-

gories of experience. More specifically, we may ask, which experience

is most important in the development of locust capture; that of pre-

capture or post-capture?

Questions like these have been raised already (Chapter 5) and

we return to them again, for they are theoretically interesting.

For instance, if we find that the post-capture experience plays a

relatively minor role, then this would imply that the act of capture

is self-reinforcing in its own right and not entirely dependent on

prey consumption for its establishment. On the other hand, if the

tendency to engage in those behaviours which lead to capture, or the

behaviours of capture per se, were liable to be strengthened through

the act of eating, then this would suggest that the post-capture

experience has reinforcing properties. Further, if the latter were

true then one might expect the response of capture to be extinguished

if a hamster was always denied the opportunity to eat.

In this chapter, then, three experiments will be reported which

shed light on these suppositions. As will be seen, the evidence

gathered suggests that eating the prey both before and after capture

has positive consequences, with the strength of the effect, in all

likelihood, being determined by the animal's genetic make-up.

8.1.   EXPERIMENT 4a

8.1a.   Design and Procedure

The subjects were 60 hamsters derived from ten litters born

between 10th August and 1st September, 1971. All were weaned between

23 and 25 days of age, weighed, sexed and placed individually in a

testing compartment. Subjects were randomly assigned to one of the

following groups: 1) Pre-Capture, 2) Post-Capture or 3) Capture.

The three groups were administered their respective treatments com-

mencing on Day 40. Treatment continued once daily until Day 50.

On Day 50 testing commenced for all subjects and it continued once

every other day (ITI of 2 days) through Day 60. In total subjects

were administered their respective treatments on ten occasions and

were subsequently tested on six occasions. The prey employed in

both the treatment phase and test phase were 4th instar locust nymphs.

The treatment administered to each group on Days 40 - 49 was as

follows:

Pre-Capture: Subjects in this group had a live locust intro-

duced into their compartment and were allowed five minutes in which

to make capture. Those which captured within this time were allowed

to hold the locust for five seconds after grasping it. Immediately

following the five second hold the locust was taken from a subject's

grasp by the Experimenter and the session terminated. Subjects in

this group were thus allowed to capture (defined as a hold on the

locust with a subject's forepaws for five seconds) but never eat.

Post-Capture: Subjects in this group were allowed to feed on

a dead locust once daily on each treatment day. This was accomplished

by proffering a dead locust that had been scalded to death about a

half-hour beforehand. Following presentation, subjects were allowed

five minutes to pick the locust up. If a subject picked the prey up

within this time it was allowed to hold it for five seconds; the prey

was then removed by the Experimenter. However, about three seconds

after removal it was then dropped back into the compartment (in the

vicinity of a subject) and a subject was then allowed an additional

five minutes to pick the locust up and eat, after which any remains

were removed. Hence subjects in this group were allowed to eat but

never capture.[1]

Capture: Subjects in this group were treated in a manner iden-

tical to that of the subjects in the Pre-Capture group, except after

taking the prey from a subject following capture (likewise defined as

---

1. The dead prey was prepared in the following manner: Prey needed
   for treatment were put into a specimen tube and boiling water
   (from an electric tea kettle) was poured into it. Immediately
   after all movement from the prey had ceased (e.g. leg twitches)
   the tube was emptied. The prey were then set on a tissue under
   an electric light in order to dry. The whole process took about
   five minutes. This method proved to be very effective, for death
   occurred instantly (hence, probably painlessly) and it did not
   disfigure the prey in any noticeable way.

a five second hold) it was then dropped back into the compartment

(about three seconds later) in the vicinity of the subject. Subjects

were then allowed an additional five minutes in which to pick it up

and eat it, after which any remains were removed. Hence subjects

in this group experienced both capture and eat.

Tests for prey capture consisted of introducing a live locust

into a subject's compartment. Subjects were then allowed a maximum

five minutes to make capture (defined during testing as a hold for

fifteen seconds) and if no capture occurred within this time the

locust was removed and the session terminated. Those who captured

were allowed an additional five minutes to eat, after which any

remains were removed.

During treatment, records were kept on the amount of prey

eaten by each individual in the Post-Capture and Capture groups and

it was also noted if subjects in the Pre-Capture and Capture groups

captured. The measures taken during testing via a multiple pen

recorder were latency to capture and the frequency of prey explora-

tion, withdrawal (from the prey), nip (at the prey) and unsuccessful

capture. Food and water were provided ad lib throughout the entire

course of the experiment.

8.1b.   Results

General Treatment of the Data. As in Experiment 1, the six

test sessions in this experiment have been combined into three

successive blocks of two each. Non-parametric statistics have been used exclusively throughout and males and females within each group have been combined.

Loss of Subjects. The mortality rate in this experiment was fairly high. As far as it could be determined, this was in no way related to the differential effects of the treatments administered. In total, 13 subjects died prior to the completion of testing. These included 5 subjects from the Pre-Capture group (M9, F4, F8, F9, F10), four from the Post-Capture group (M8, F2, F8, F9) and four from the Capture group(M10, F7, F9, F10).

Behaviour During the Treatment Phase. With the exception of two subjects (M4 and F2) all in the Pre-Capture group captured on at least one occasion during treatment. Several subjects in this group failed to capture on the last few sessions after having earlier captured; a few showed reversals of the reaction (i.e. capture followed by no capture on successive treatments) and a few captured on all ten treatment days. In general, no consistent pattern emerged among the subjects in the Pre—Capture group during the course of the ten treatments.

The incidence of capture for the subjects in the Capture group during treatment increased substantially over the ten treatment days. At first, not many captured but most came to capture on the last few sessions. In total, only two subjects from this group failed to make a single capture during the entire course of treatment.
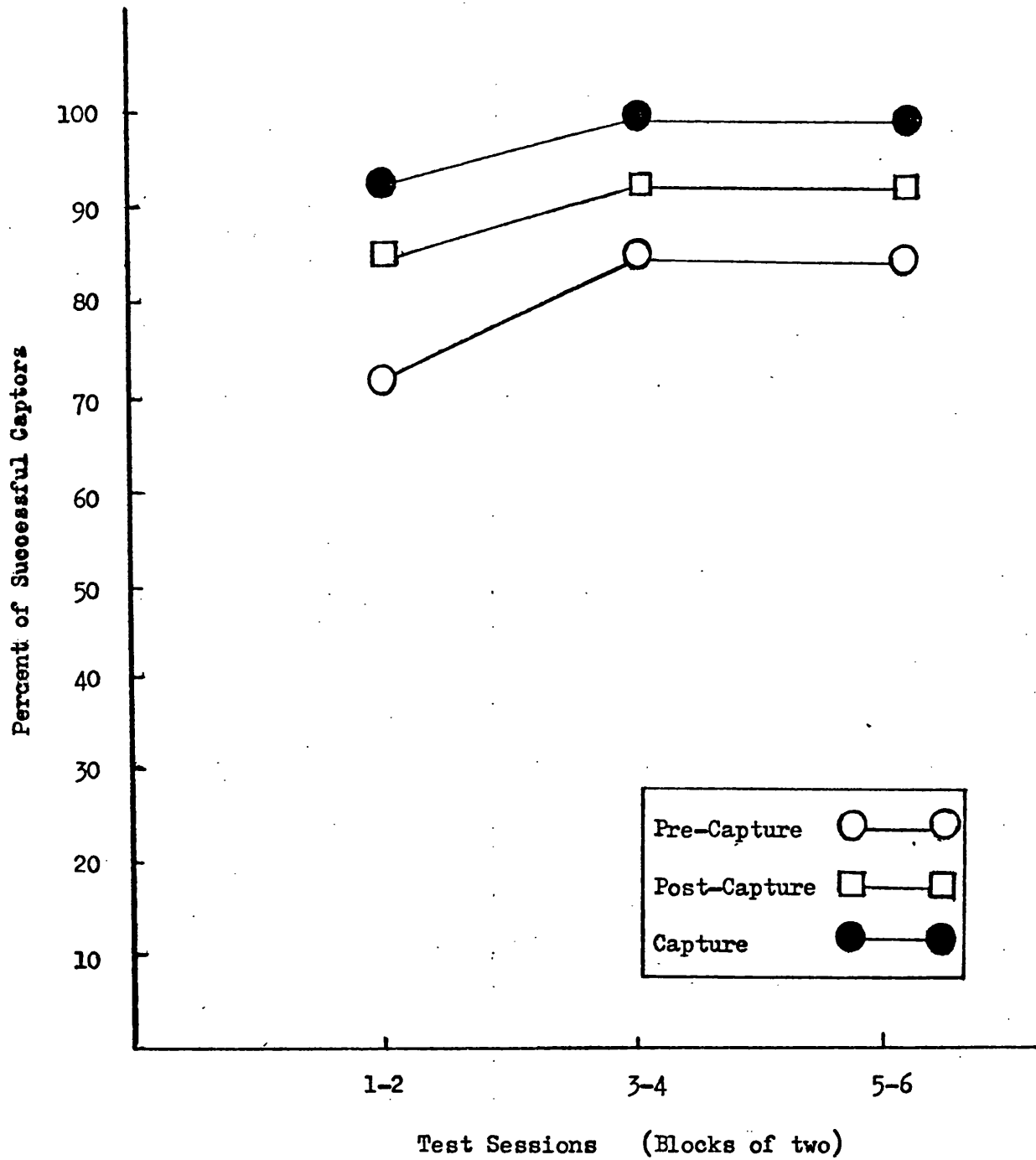
Figure 8.1. Percent of successful locust captors for the three treatment groups in Experiment 4a, males and females combined. Test sessions have been combined into successive blocks of two.

Nearly all subjects in the Post-Capture group ate the dead

locust on all ten treatment days. Ambivalence towards the prey

was not as great as the ambivalence of the subjects in the other

two groups. In general, Post-Capture subjects showed hesitancy when

first presented with the dead locust but eventually most came to eat

at least part of the prey either on treatment days one or two. The

behaviour of one subject (M7) in this group which failed to eat on

any occasion was markedly abnormal. This subject, subsequent to

weaning and during the treatment and test phases, continued to turn

persistently in circles during most of its waking hours. Consequent-

ly, on the whole, during treatment and during the tests M7 remained

oblivious to the presence of the prey after it was proffered to it.[2]

Percent of Captors. Raw data in terms of latency to capture

for the 47 subjects who completed testing appears in Appendix B,

Table 12. Subjects which failed to capture were assigned the score

of 300 seconds. Inspection of Figure 8.1 shows that all subjects in

the Capture group captured on blocks two and three. This incidence

was higher than that of the Post-Capture group which, in turn, had a

higher incidence than the Pre-Capture group. Further examination of

---

2. This 'vicious circle behaviour' which I call it, and not to be
   confused with the term coined to describe a certain type of avoid-
   ance learning paradigm (see Gray, 1971) is worth noting, for it
   has yet to be described in the hamster literature. Again, for
   emphasis, what this subject did was to persistently turn in circles,
   both in a clockwise and counter-clockwise direction, during most of
   its waking hours. During the course of this research project this
   author has witnessed this behaviour in only one other hamster, a
   male. Whether it be the result of a genetic anomaly or a brain
   disfunction is an open question. J.H.Mackintosh (personal commun-
   ication, 1974) notes that it occurs in captive voles.

Figure 8.2. Mean delay between presentation and capture of a locust for each treatment group in Experiment 4a, males and females combined. The six test sessions have been combined into successive blocks of two.

Table 8.1.Comparisons between latency to capture on any two
test blocks for the three treatment groups in Experiment 4a.
The six test sessions have been combined into three successive
blocks of two each. The figure in brackets within each cell
indicates the mean latency to capture (in sec) for the two
blocks being compared and the unbracketed figure indicates the
probability that the two latencies differ significantly from each
other as determined by the Sign Test where $p=q=\frac{1}{2}$. Latency scores
for the males and females within each group have been combined.
All probabilities are based on two-tailed tests.[a]

TREATMENT GROUP	TEST BLOCK COMPARISONS					
	1 vs 2		1 vs 3		2 vs 3	
PRE-CAPTURE (n=15)	(318)	(213)	(318)	(217)	(213)	(217)
	.73		.90		.01	
POST-CAPTURE (n=16)	(222)	(167)	(222)	(171)	(167)	(171)
	.97		.73		.21	
CAPTURE (n=16)	(122)	(155)	(122)	(140)	(155)	(140)
	.19		.19		.21	

[a]The probability values listed are the inverse of those values
listed in Table D of Siegel (1956, p-252). Thus a value of .97 is
significant at the .03 level.

Figure 8.1 shows that the incidence increased slightly in all groups over the three test blocks.

Latency to Capture. In Figure 8.2 the mean latencies to capture are graphically presented for all groups. Examination shows that the Capture group, on average, took roughly just over 100 seconds to capture on each test block. This contrasts markedly with the latency scores for the Pre-Capture group. For example, on block one, Pre-Capture subjects captured with an average latency of over 300 seconds and on blocks two and three this decreased somewhat and stabilized out to roughly 200 seconds. Post-Capture subjects also captured with a considerably higher latency than subjects in the Capture group on block one; however, like the Pre-Capture group, latencies for the Post-Capture group also dropped substantially on blocks two and three. As a result latencies for the Post-Capture group were marginally different than those for the Capture group on the latter two test blocks.

Sign tests were conducted to determine if significance existed (in terms of latency) between the blocks for any group. The results of the analysis appear in Table 8.1. Inspection shows a lack of significance between any block within any group with the exception of block one versus two for the Post-Capture group. Specifically, subjects in this group captured with a significantly shorter latency ($p < .03$, two-tail test) on block two.

More importantly, however, there were significant differences

Table 8.2.Comparison between the different treatment groups of
Experiment 4a in terms of latency to capture on each of the three
test blocks. The six test sessions have been combined into three
successive blocks of two each. The bracketed figures within each
cell indicate the mean latency to capture (in seconds) for the
two groups being compared and the unbracketed figure indicates
their respective U score as determined by the Mann-Whitney U test.
Males and females within each group have been combined. All
probabilities are based on two tailed tests.

TEST BLOCK	GROUP COMPARISONS		
	Pre vs Post	Pre vs Cap	Post vs Cap
1	(318) (222) 132.5	(318) (122) 60.5^a	(222) (122) 58^a
2	(213) (167) 111.5	(213) (155) 103	(167) (155) 123.5
3	(217) (171) 106.5	(217) (140) 70^b	(171) (140) 104

$^a p < .02$ $^b p < .05$

Figure 8.3. Mean frequency of exploration, withdrawal, nip and unsuccessful capture for the three treatment groups in Experiment 4a. Means are based on the cumulative frequency of each behaviour over the six test sessions. Frequency scores for the males and females within each group have been combined. (Pre-Capture; Post-Capture; Capture)

Table 8.3. Comparison between the Pre-Capture, Post-Capture, and Capture groups of Experiment 4a in terms of the cumulative frequency of exploration, withdrawal, nip, and unsuccessful capture over the six test sessions. The bracketed figures within each cell indicate the mean (of the cumulative total) frequencies for the two groups being compared and the unbracketed figure indicates their respective U score as determined by the Mann-Whitney U test. Males and females within each group have been combined. All probabilities are based on two-tail tests.

BEHAVIOUR	GROUP COMPARISONS		
	PRE vs POST	PRE vs CAP	POST vs CAP
EXPLORATION	(23.0) (30.0) 95.5	(23.0) (18.6) 100.5	(30.0) (18.6) 74.5^a
WITHDRAWAL	(4.2) (5.8) 100.5	(4.2) (.81) 87.5	(5.8) (.81) 62^b
NIP	(12.8) (17.8) 79.5	(12.8) (11.5) 107.5	(17.8) (11.5) 70.5^a
U. CAPTURE	(4.0) (6.3) 90	(4.0) (3.6) 110	(6.3) (3.6) 90.5

[a] $p < .05$

[b] $p < .02$

between groups on two of the test blocks. Results indicating these

differences, as determined by two-tail Mann-Whitney U tests, appear

in Table 8.2. Inspection shows that on block one the Capture group

differed significantly from both the Pre-Capture and Post-Capture

group. No significance was present between any group on block two,

but again on block three significance emerged between the Pre-Capture

and Capture group.

Frequency of Exploration, Withdrawal, Nip and Unsuccessful

Capture. Raw data in terms of the frequency of each of these behav-

iours appear in Appendix B, Table 13 (exploration), Table 14 (with-

drawal), Table 15 (nip) and Table 16 (unsuccessful capture).

Statistical analysis was made on the cumulative frequency of each

of these behaviours over the six test sessions. In Figure 8.3 the

means (of the cumulative total for all the subjects within a group)

are graphically presented for each group, and the results of the

Mann-Whitney U test indicating significance between groups for each

behaviour are presented in Table 8.3. As the results show, subjects

in the Post-Capture group exhibited significantly more exploration,

withdrawal and nip than subjects in the Capture group. Other than

this no significance was present between the Pre-Capture and Capture

group (although note that the mean frequency of withdrawal for Pre-

Capture subjects was four times as great) or between the Pre-Capture

and Post-Capture group for any behaviour.

8.1c. Discussion

The results of this experiment may be summarized as follows:

1) The Pre-Capture and Post-Capture groups showed a significantly higher latency to capture than the Capture group on test block one. Significance was also achieved between Pre-Capture and Capture subjects on test block three but not on two. Differences between the Pre-Capture group and Post-Capture group failed to reach significance on any block; however, Pre-Capture subjects consistently captured with a higher latency on all three blocks.

2) In terms of the frequency of exploration, withdrawal, nip and unsuccessful capture, the Post-Capture group differed significantly from the Capture group on most behaviours. On the other hand, differences between the Pre-Capture group and Capture group were marginal.

The fact that latency scores for the Capture group were significantly lower than the latencies for the Pre-Capture group on blocks one and three suggests that prey removal after capture had the effect of decreasing the likelihood of capture. Conversely stated, and more simply, this result suggests that eating the prey after a capture was reinforcing.

Concerning this assertion it should be noted that the act of capture for the subjects in the Pre-Capture group did not become extinguished (as expected) but rather became less likely to occur

as reflected in the higher latencies (Figure 8.2). Qualitative

observation of the behaviour of Pre-Capture subjects during the

last few treatment sessions suggests that their relatively high

latencies were probably in part due to the ambivalent way in which

they reacted to the prey. Compared with the behaviour of most

subjects in the Capture group (most Capture subjects usually attemp-

ted capture immediately after detecting the prey on block one)

Pre-Capture subjects often hesitated after exploration (as reflected

in the relatively long duration of exploration[3]) or showed indiffer-

ent behaviour and, on occasion, withdrawal. Pre-Capture subjects

who behaved in this manner did, however, on some occasions capture

towards the end of one of the five minute test sessions on block

one (see raw data, Appendix B, Table 12). Thus, for this reason

latencies to capture for Pre-Capture subjects were significantly

higher than those for Capture subjects on block one; however, in

terms of incidence it was roughly the same (see Figure 8.1).

On test block one, then, the majority of Pre-Capture subjects

captured with relatively high latencies. For this reason it would

be feasible to argue that the tendency to capture for Pre-Capture

subjects was not as strong on block one as it was for subjects in

the Capture group. Therefore prey removal after capture probably

had the effect of dampening the motivation for capture, or more

technically speaking, weakening the bond - but not entirely extin-

guishing it - between the stimulus of elicitation (e.g. the prey)

and the response (e.g. prey capture).

---

3. These data were collected but will not be reported.

Further, it is important to realize that Pre-Capture subjects

were allowed to consume the prey (if they captured) during the test

sessions (an experience which they were always denied during treatment).

As a result, these eats which they experienced on block one probably

served to diminish any ambivalence they still had towards the prey.

Consequently, with the diminished ambivalence the tendency to capture

was increased. Pre-Capture subjects thus came to capture with a

shorter latency and for that matter a higher incidence on test

blocks two and three. On block three, however, it should be noted

that their latency was still significantly higher (p $<$ .05) than

that of the Capture group.

On the other hand, in addition to the beneficial effects

derived from the post-capture experience, the pre-capture experience,

likewise, probably acted in a positive fashion. Specifically, as it

was argued in Chapter 5, the experience of confrontation with live

prey probably serves in the first instance to habituate a hamster's

fear of the novel locust and, secondly, it provides the opportunity

for perfection of those behaviours needed for capture. The credence

of these two suppositions can be more fully understood if Table 8.3

is re-examined. As indicated, the Post-Capture group (subjects in

this group had no prior experience with the live locust prior to

testing) had significantly higher frequencies than the Capture group

for three of the behaviours (exploration, withdrawal and nip;

differences in the frequency of unsuccessful capture, although large,

fell short of significance). Further, it should be noted that the

Post-Capture group had considerably higher frequencies (although not

significant) than Pre-Capture subjects for all behaviours. And lastly, differences in the frequency between the Pre-Capture and Capture group were minimal for all four behaviours. Thus, these differences between Post-Capture and Capture subjects, and between Post-Capture and Pre-Capture subjects, may be understood in terms of the lack of the pre-capture experience for the Post-Capture subjects prior to test onset. As would be expected, Post-Capture subjects lacking such experience behaved in a manner typical of a hamster attempting capture for the first time; hence, the relatively high frequencies.

Thus, the differences in frequency provide some indication of the functional significance of the pre-capture and post-capture experiences. In summary, to account for the differences between the Post-Capture group and the other two groups is not difficult if one realizes that Post-Capture subjects were simply not given the opportunity to perfect those behaviours required for an efficient capture. During treatment the only kind of locust these subjects encountered was a dead one - never a live one. Consequently, during the tests, subjects in the Pre-Capture and Capture groups (having earlier benefited from their experience with the live locust during treatment) needed fewer explorations, nips and unsuccessful captures to make capture.

A more vexing problem would be to offer a satisfactory explanation for the small difference between the Pre-Capture and Capture groups in terms of frequency; at the same time one would have to offer a satis-

factory explanation for the large difference in latency between

these two groups. Possibly each of these results could be understood

in terms of the great individual differences in the susceptibility to

the effects of prey removal after capture. That is to say at one

extreme some subjects in the Pre-Capture group seemed impervious to

the effects of prey removal; at the other, this treatment seemed

to have the unmistakable effect of considerably decreasing the

chances of capture. Therefore, the captors and non-captors of the

Pre-Capture group (i.e. those who captured during most treatment

sessions along with those who captured at first but then subsequent-

ly failed to do so) had probably both benefited from the experience

gained during treatment in that they were each allowed sufficient

exposure to the live locust so that their fear could habituate and,

further, enough practice at capture so that they could become

efficient captors. It therefore seems likely that the pre-capture

experience acted in the same way for the Pre-Capture group as it

did for the Capture group. But, as we know, Pre-Capture subjects

had the prey removed after capture during treatment; this in turn,

as previously mentioned, probably acted to increase ambivalence and

therefore to reduce the tendency to capture. Hence, although Pre-

Capture subjects possessed the behaviours needed to make an efficient

capture, they also, concomitantly, probably possessed a weaker

tendency to capture. Overall, then, this was reflected in relatively

low frequencies accompanied by relatively high latencies. Further,

the fact that Pre-Capture subjects showed a relatively high incidence

of withdrawal when compared with the Capture subjects does not negate

the influence the pre-capture experience had on the habituation of

the fear response, but rather is suggestive of a renewed increase in ambivalence. This ambivalence is interesting, for it is suggestive of a conflict between capture and the learnt inhibition of not capturing.

If our theory holds then, i.e. the pre-capture experience serves to reduce fear, and secondly to perfect the behaviours needed for capture, while the post-capture experience serves mainly to increase the tendency to capture, or more generally speaking increase the motivation for capture, then we could expect Post-Capture subjects to show relatively low latencies accompanied by relatively high frequencies. Again examination of Table 8.2 and Table 8.3 shows that this was the case. Therefore, this result and the results discussed above suggest that eating prey both before and after capture increases the chances of capture on subsequent occasion.[4]

An important point to note before bringing this dicussion to a close is that both the pre-capture and post-capture experiences together, as they occurred for the subjects in the Capture group, were more beneficial than either one alone. They were beneficial in the sense that they enabled the Capture subjects to capture with short latencies (compared with Pre-Capture subjects) and low

---

4. The mean by which the post-capture experience increases the tendency to capture will be discussed in Chapter 9, Section 9.3c. However, at this stage in our analysis, we may further speculate that for post-capture subjects this experience, in addition, might have the secondary function of fear reduction.

frequencies (compared with Post-Capture subjects). It therefore seems that each of these independent experiences act together, in an additive fashion, in the development of locust capture by hamsters.

8.2.   EXPERIMENT 4b

The next experiment to be reported, 4b, may be viewed as a replication of Experiment 4a with some important modifications in design and procedure. The modifications were as follows:

1) Experiment 4a lacked a control group; that is, a group that had no experience with the prey in any form prior to testing. It therefore seemed worthwhile to compare the performance of pre-capture and post-capture subjects with the performance of naive subjects in order to show conclusively that each treatment on its own had a positive effect. Hence, a control group has been included in Experiment 4b.

2) Experiment 4b also sought to explore the temporal relationship between capture and eat. Specifically, it was asked, what would the effects be if a hamster was always denied the opportunity to eat immediately after a capture and, instead, allowed to eat only after some time had passed since capture ? In other words, did eat have to be temporally contiguous with capture in order for the predatory response to develop or could these two events be temporally dissociated ?

3) In addition to these two new objectives Experiment 4b was conducted to see if a more pronounced effect from the pre-capture treatment could be obtained. It may be recalled that the results of Experiment 4a suggested that prey removal after capture had the effect of dampening the motivation for capture, but, as the statistical analysis revealed, this effect was only marginally significant. In view of the theoretical importance attached to what effects the post capture experience might have, an attempt was made in Experiment 4b to increase the magnitude of this effect (with the hope of extinguishing the capture response outright) by doubling the dose of treatment.

8.2a.   Design and Procedure

The subjects were 60 hamsters derived from eleven litters born between 7th November, 1971 and 27th February, 1972. All were weaned between 23 and 25 days of age, placed in an individual compartment and randomly assigned to one of the following groups: 1) Pre-Capture, 2) Post-Capture, 3) Capture; 4) Pre-Post and 5) Control. The four experimental groups (Controls excluded) were administered their respective treatments commencing on Day 40 and treatment continued twice daily until Day 50. On Day 50 testing commenced for all subjects and it continued once every other day for six successive days. In total, subjects were administered their respective treatments on 20 occasions and were subsequently tested on six occasions. The prey employed in both the treatment and test phase were 4th instar locust nymphs. The design of the experiment

Table 8.4. Design of Experiment 4b.

Condition	Treatment (Days 40 - 49)	Test (Days 50-52-54-56-58-60)
Group 1 (Pre-Capture)	Capture minus Eat	Live locust
Group 2 (Post-Capture)	Eat minus Capture	Live locust
Group 3 (Pre-Capture & Post-Capture)	Capture plus Eat	Live locust
Group 4 (Pre-Capture & Post-Capture)	Capture delay eat	Live locust
Group 5 (Neither Pre- nor Post-Capture)	Control	Live locust

is presented in Table 8.4.

The treatment administered to the Pre-Capture, Post-Capture and Capture groups was identical to the treatment administered to these groups in Experiment 4a except, as indicated, it occurred twice per day rather than once per day. The interval between the two daily treatments was approximately one hour. Subjects in the Pre-Post group were treated in a fashion similar to that of the subjects in the Pre-Capture group; however, Pre-Post subjects, in addition, were presented a dead locust approximately 15 minutes after each treatment (regardless of whether they captured or not). They were allowed a maximum of five minutes for eat, after which any remains were removed. Pre-Post subjects were thus given the opportunity to experience the pre-capture and post-capture treatments independently. Subjects in the Control group were not exposed to the locust prior to Day 50. On Day 50 testing commenced for this group, and for the other four groups, and it was identical in all respects to the testing procedures carried out in Experiment 4a.

8.2b.   Results

General Treatment of the Data. Unlike the latency data in the previous experiment latency scores for this experiment have not been blocked into groups of two. Instead, latency scores for each test session have been treated separately. This change in analysis was necessary because preliminary analysis showed that blocking latencies obscured differences between treatment groups. Aside from this, the

data was treated in a similar fashion to the data of Experiment 4a in that the sexes within each group were combined and the statistical tests employed were exclusively of the non-parametric type.

Loss of Subjects. Those subjects who failed to complete testing due to death subsequent to weaning and prior to the completion of testing included: one subject from the Pre-Capture group (M6); three subjects from the Post-Capture group (M1, M5, F6); one subject from the Capture group (M6); three subjects from the Pre-Post group (M3, F3, F5) and one subject from the Control group (F3). In total 51 subjects completed testing; these included 11 subjects each from the Pre-Capture, Capture and Control groups and 9 subjects each from the Post-Capture and Pre-Post groups. Raw latencies to capture appear in Appendix B, Table 17.

Behaviour During the Treatment Phase. The incidence of capture for Pre-Capture subjects was inconsistent over the ten treatment days; that is to say, reversals occurred in that some subjects captured on one treatment day followed by no capture on the next. On the other hand, a few captured on all 20 treatments. All, however, captured on at least two occasions. Generally speaking, as in Experiment 4a, there was an overall increase in capture latency coupled with a decrease in incidence towards the latter part of treatment. Post-Capture subjects, with the exception of one, ate the dead prey proffered on all 20 treatments. Likewise, most subjects in the Capture group and Pre-Post groups captured on the majority of the treatment sessions. Further, all Pre-Post subjects ate the dead prey on most occasions during treatment.
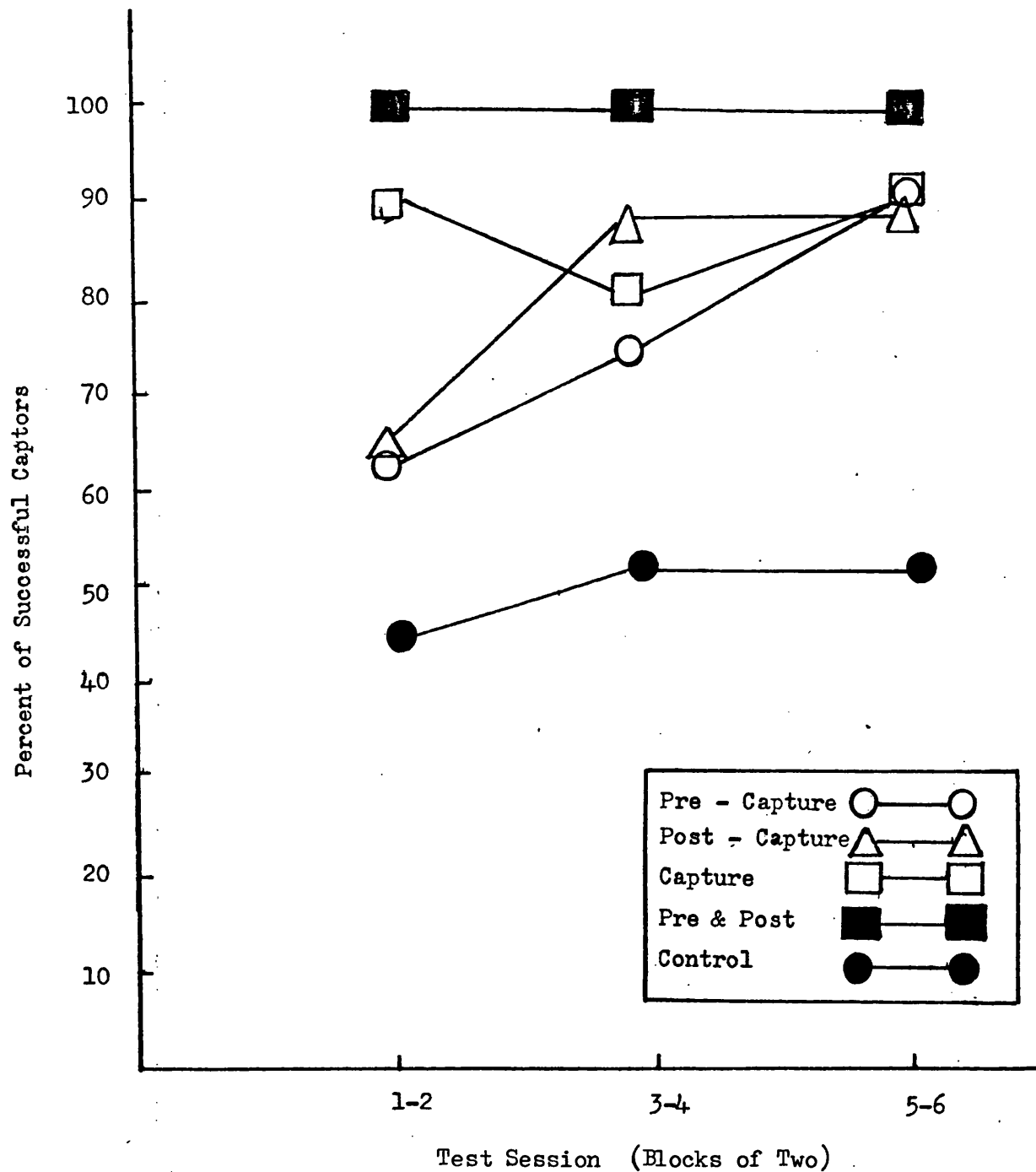
Figure 8.4. Percent of successful locust captors in the five treatment groups of Experiment 4b. Males and females within each group have been combined. The six test sessions have been combined into successive blocks of two.
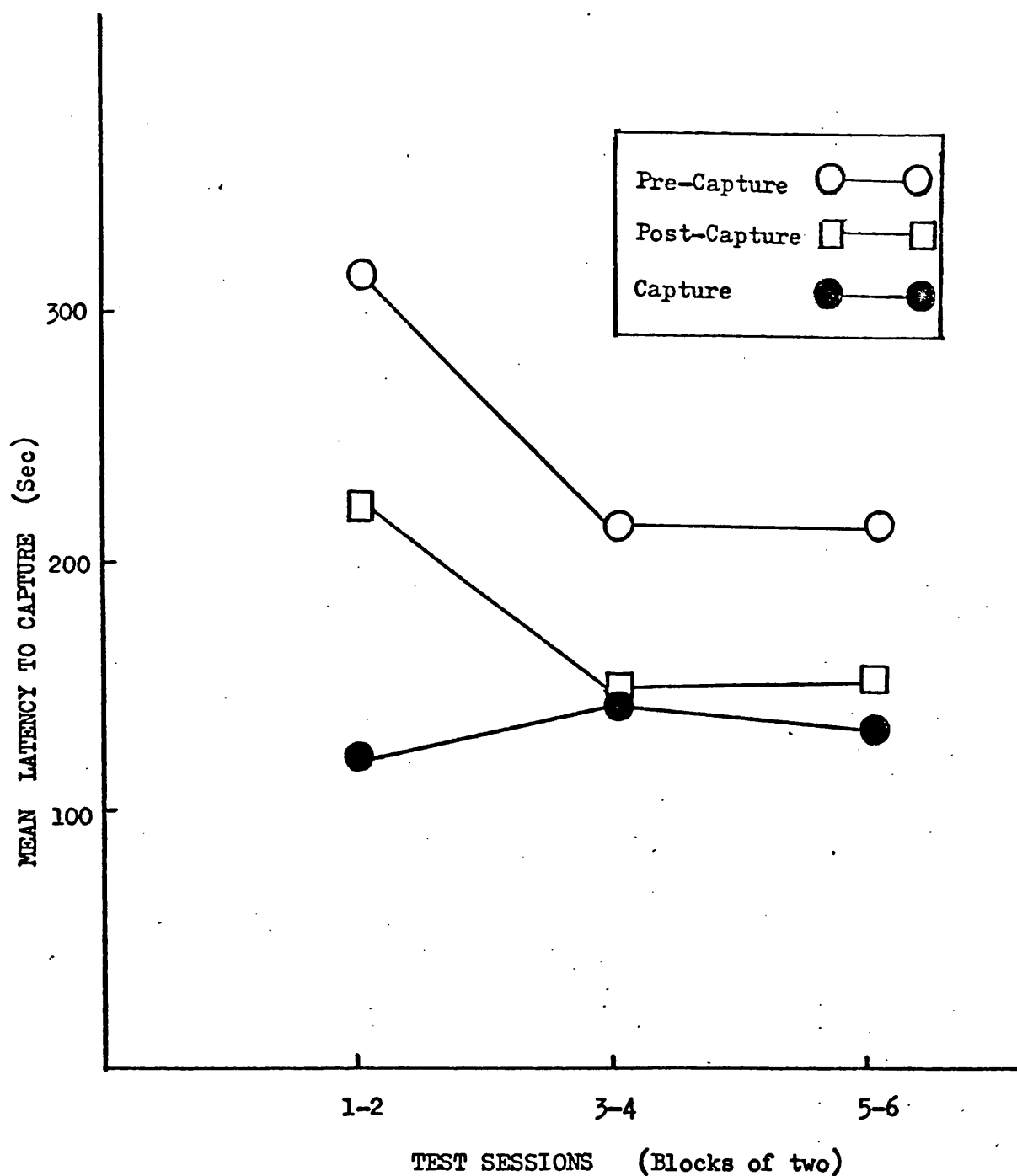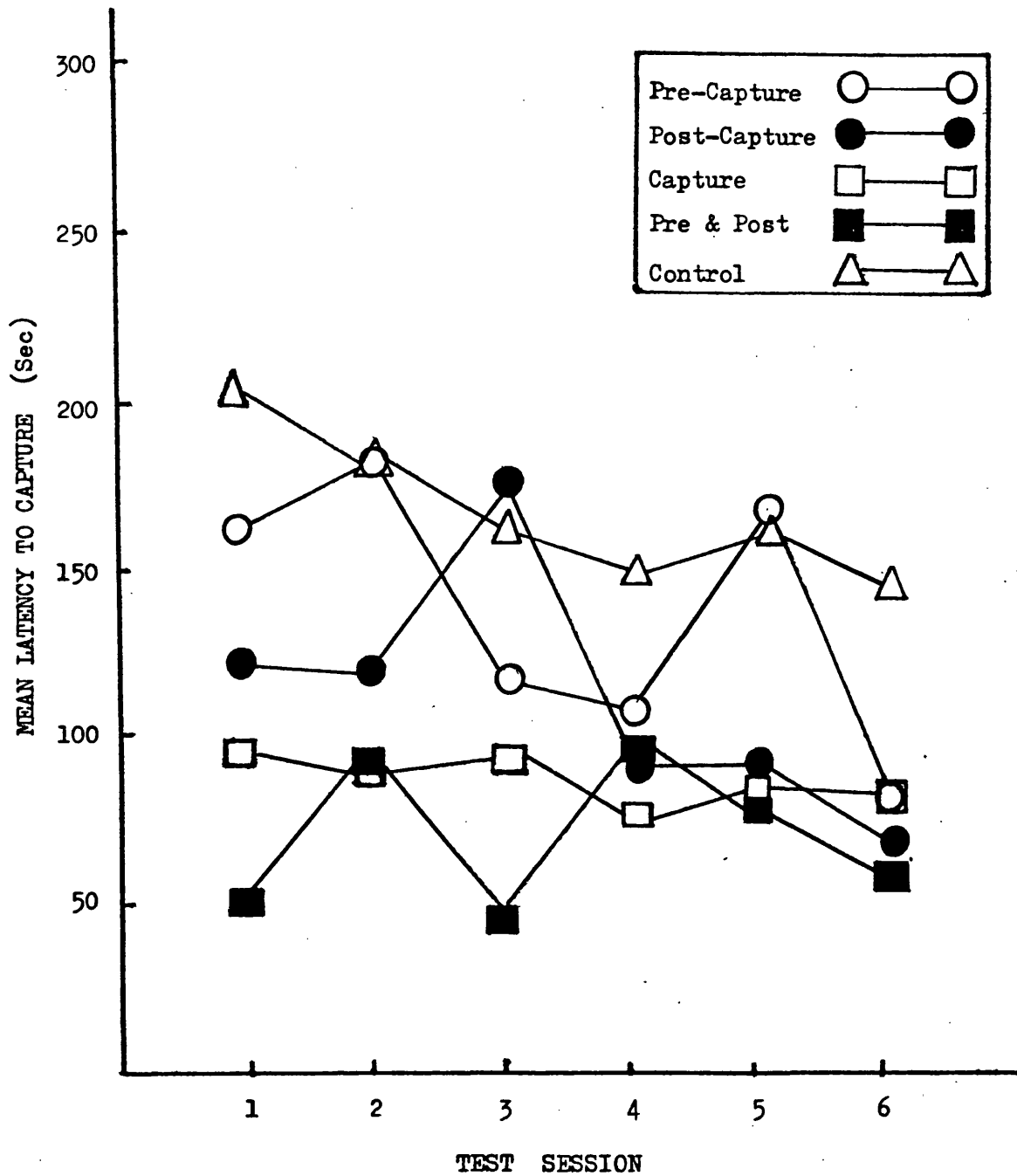
Figure 8.5. Mean delay between presentation and capture of a locust for each treatment group in Experiment 4b, males and females combined.

On the whole, subjects in the Pre-Capture, Capture and Pre-

Post groups reacted passively to prey removal after capture. In

only a few instances did they actually attempt to keep the prey

from the Experimenter by holding it in their mouths. In most cases

when the Experimenter inserted his hand into a compartment to remove

the prey, subjects reacted by dropping the locust and moving off to

another part of the compartment. In short, taking the prey from a

subject after capture did not seem to be very disturbing.

Percent of Captors. Figure 8.4 graphically depicts the percent

of captors in each of the five groups over the six test sessions.

For the purpose of this particular presentation the six test ses-

sions have been blocked into groups of two. Inspection shows that

on block one there was a 100% and 90% incidence of capture for the

subjects in the Pre-Post group and Capture group, respectively.

This was somewhat higher than the incidence in the Pre-Capture and

Post-Capture groups (64% and 67% respectively) and considerably

higher than the incidence in Control group (49%). On blocks two

and three the Post-Capture group continued to capture with a 100%

incidence while the incidence in the Capture group remained about

90%. The incidence of capture for the Pre-Capture and Post-Capture

subjects increased on block two and on block three it was nearly

identical to that of the Capture group. The incidence in the Control

group remained relatively low on blocks two and three (50% on each).

Latency to Capture. In Figure 8.5 the mean latencies to capture

on each of the six test sessions for all groups are graphically pres-

Table 8.5. Summary of the Kruskal-Wallis one-way analysis of variance for latency to capture on each of the six test sessions in Experiment 4b.

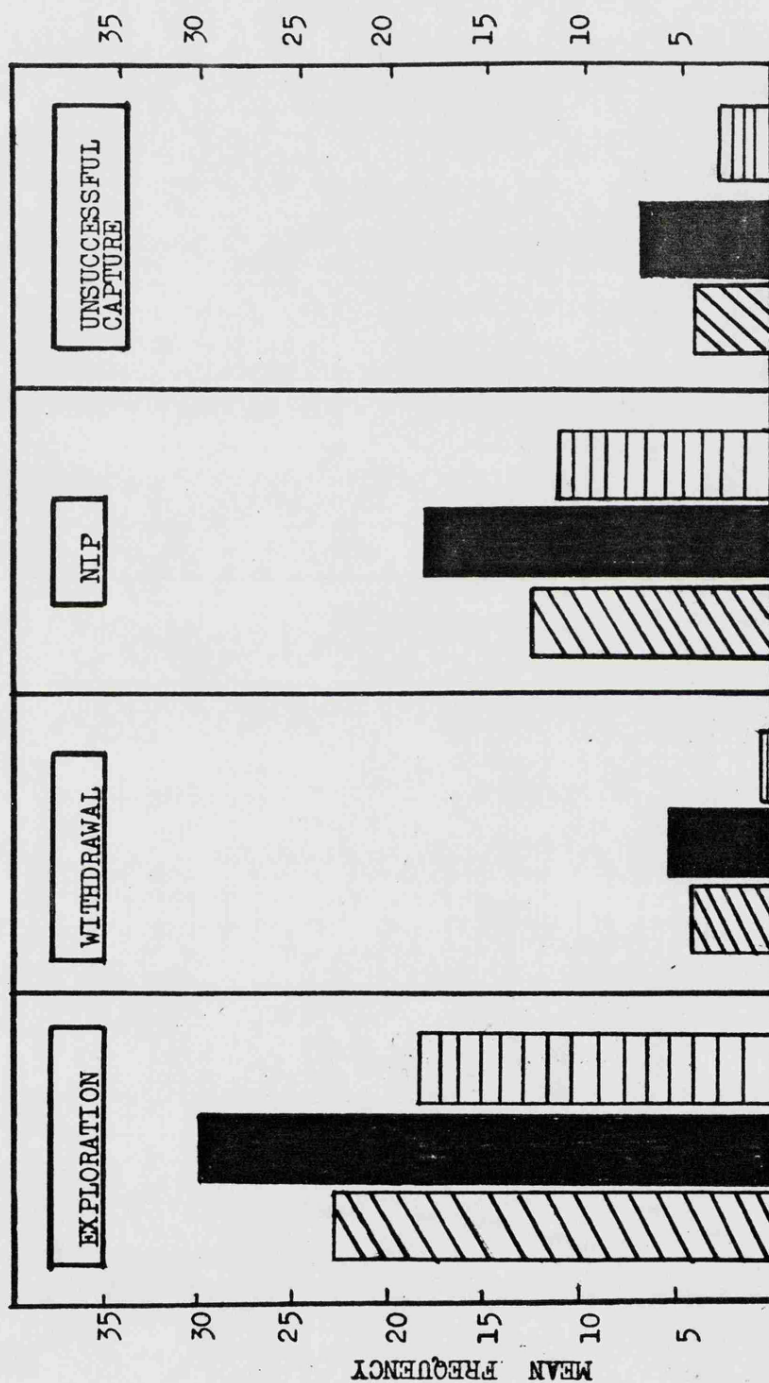| TEST SESSION	H VALUE	df	PROBABILITY
1	23.85	4	$<$.001
2	8.36[a]	4	$<$.10
3	15.16	4	$<$.01
4	13.90	4	$<$.01
5	13.89	4	$<$.01
6	18.49[a]	4	$<$.001

[a]corrected for ties

Table 8.6. Frequency of exploration, withdrawal, nip and unsuccessful capture for each treatment group in Experiment 4b, males and females combined. Frequency scores for the six test sessions have been pooled and the overall mean presented. The column on the extreme right indicates the probability that the five groups differ significantly for the behaviour in question as determined by the Kruskal-Wallis one-way analysis of variance (two tail). See text for further details.

Behaviour	Pre-Capture	Post-Capture	Capture	Pre & Post	Control	Probability
Exploration	38.0	35.0	20.0	27.3	27.4	$< .001$
Withdrawal	6.0	5.3	4.0	2.0	6.4	NS
Nip*	16.2	16.8	13.7	14.3	13.8	NS
U. Capture*	6.5	7.3	5.2	4.7	3.3	NS

*Only those subjects which captured on at least on occasion were included in the analysis.

ented. A summary of the statistical analysis performed on this

data (a Kruskal-Wallis one way analysis of variance) is presented

in Table 8.5. As Table 8.5 indicates the five groups differed

significantly on five of the six test sessions. Visual inspection

of Figure 8.5 shows that, relatively speaking, latencies for the

Control group were high on all six test sessions; however, as

indicated, there was a slight tendency for the latencies in this

group to decrease with successive tests. In similar fashion,

latencies for the Post-Capture and Pre-Capture groups also decreased

on the last few sessions. Further, inspection shows that the Capture

and Pre-Post groups had lower latencies than either the Pre-Capture

or Post-Capture groups on most test sessions. The Post-Capture group

in turn had lower latencies than the Pre-Capture group on five of

the six test sessions.

Frequency of Exploration, Withdrawal, Nip and Unsuccessful

Capture. Raw data in terms of frequency for each behaviour appears

in Appendix B, Table 18 for exploration, Table 19 for withdrawal,

Table 20 for nip and Table 21 for unsuccessful capture. The means

are presented in Table 8.6, along with the results of the Kruskal-

Wallis one-way analysis of variance. As expected, the frequency of

exploration and withdrawal differed considerably among the groups

although, as indicated, the difference in withdrawal did not reach

significance with a two-tail test. Statistical analysis of the

frequency of nip and unsuccessful capture was made on the scores

of only those subjects who captured on at least one occasion. Those

subjects which failed to capture were excluded because they rarely

nipped or attempted capture. Surprisingly, as the results show, the

difference between groups for these two behaviours were negligible.

8.2c. Discussion

The results of this experiment corroborate the findings of

Experiment 4a. In summary, this experiment showed that:

1) On sessions one and two latencies to capture for the Pre-

Capture subjects were relatively high when compared with the scores

for the Capture and Pre-Post subjects. Statistical significance, in

terms of latency, emerged among the groups on session one, and sig-

nificance was nearly achieved on session two (p < .10). Therefore,

as Experiment 4a suggested, prey removal after capture probably had

the effect of weakening the tendency to capture for Pre-Capture

subjects. Doubling the amount of treatment administered prior to

a test did not seem to produce a more pronounced effect.

2) As was the case in Experiment 4a, Pre-Capture subjects which

captured during testing (and hence were allowed to eat) eventually

came to capture (on the latter test sessions) with latencies compar-

able with those of the other treatment groups. The eats these

subjects experienced during testing were therefore clearly beneficial.

3) Relative to the Control group, subjects who experienced

either the Pre-Capture or Post-Capture treatments, or both, captured

with shorter latencies on most of the latter test sessions. Post-

Capture subjects, in turn, consistently had shorter latencies than

Pre-Capture subjects on most test sessions (with the exception of

session three) and on the early test sessions; the Pre-Post and

Capture groups consistently had shorter latencies than either the

Pre-Capture or Post-Capture groups. Therefore, these findings suggest

that each treatment on its own had some positive effect (when compared

to no treatment at all); both treatments experienced together, how-

ever, resulted in a more rapid development of the predatory response.

4) The act of eat and that of capture do not have to be

temporally connected in order for the predatory response to develop.

In fact comparing the latencies of the Pre-Post group with those of

the Capture group suggests, if anything, that separating these two

events in time had slightly positive consequences. Therefore, it

seems that prey consumption does not have to immediately follow prey

capture in order to strengthen the response of capture (see Hogan,

1973a, 1973b who has described a similar phenomenon).

In addition to the above it seems feasible to argue that the

relative importance of the post-capture experience depends, to a

large degree, on an animal's predisposition to capture. This suppos-

ition comes to the forefront if one considers the large individual

differences in the tendency to capture between subjects in the Pre-

Capture group. To reiterate, prey removal after capture seemed to

affect some subjects considerably more than others. Specifically,

some stopped capturing altogether, or captured with a higher latency,

while others continued to reliably capture despite the fact that they

were never given the opportunity to eat. Apparently, then, for some,

the pre-capture experience is all that is needed for the development

of the predatory response. The fact that this experience has positive

consequences, suggests, as previously mentioned, that on its own it

acts as a self-reinforcer.

To test this important hypothesis, two distinct populations of

hamsters would be needed. Ideally, one population would consist of

subjects which possessed a strong tendency to capture, and the

second conversely, of subjects which possessed a weak tendency to

capture. The crucial test would allow only some subjects within

each population to eat after capture; others would be denied this

same experience. In the next experiment, 4c, an attempt was made

along these lines.

8.3. EXPERIMENT 4c

If our hypothesis is correct then prey removal after capture

should have negligible effects on hamsters possessed with a predis-

position to capture. On the other hand, this same treatment should

have the effect of making capture less likely, or extinguishing it

altogether, in hamsters that were predisposed not to capture.

8.3a. Design and Procedure

The 16 subjects which served in this experiment were derived

from two strains, the first of which was selectively bred for the

tendency to capture (formerly referred to as the Captor strain),

and the second selectively bred for the opposite tendency; i.e.

failure to capture (referred to as the strain of Non-Captors).

Details of the methods employed in each of the breeding programmes

will not be presented here, for they will be covered in detail in

Chapter 11. It will suffice for now to say that the ten Captors

and six Non-Captors selected for this experiment came from the

eighth generation of their respective strains; i.e. the eighth

generation of Captors and the eighth generation of Non-Captors.

As will be seen, the experiments in Chapter 11 have shown that this

breeding programme was highly effective in selecting for the desired

traits.

All subjects were born between 12th December, 1973 and 8th

February, 1974. All were weaned from their respective litters

between 23 and 25 days of age and placed in an individual testing

compartment. Subjects were then given a ten minute test for locust

capture with a 4th instar locust commencing on Day 40. Subjects who

captured within this time were allowed to hold the locust for 15

seconds after grasping it (a successful capture for the criterion

test was defined as a hold on the locust with a subject's forepaws

for at least 15 seconds). It was then removed by the Experimenter

and the session terminated. Thus, subjects after their initial

capture were not permitted to eat. Subjects who failed to capture

on Day 40 were again tested in a similar manner on Days 41 and/or 42.

The ten Captors and six Non-Captors selected for this experiment all

met the criterion of capture when tested on either Day 40, 41 or 42.

Following their initial capture, subjects from both the Captor

strain and Non-Captor strain were assigned to either one of two

conditions: eat following capture, or no eat following capture.

Testing then began on the day following the initial criterion test

and continued twice daily for six successive days.   On each test

session subjects were allowed two minutes in which to make capture;

if no capture occurred within this time the locust was removed and

the session terminated.   Those subjects who captured were allowed

to hold the locust   for five seconds only (a successful capture

during the test sessions was re-defined as a hold for five seconds).[5]

It was then removed by the Experimenter and the session terminated.

However, those subjects within each strain who were allowed to eat

following capture had the maimed locust immediately put back into

their compartment (in the vicinity of the, subject);   it was then

left there until it was consumed, or until the next test session.

The interval between successive test sessions on each test day was

approximately 30 minutes.   A stopwatch was used to time the length

of each test session.

8.3b.   Results

The raw incidence of capture over the 12 test sessions for

the Captors and Non-Captors in each treatment condition appears in

Appendix B, Table 22.

---

5.   During the tests the duration of hold necessary for a
     successful capture was shortened to five seconds in order to
     reduce the likelihood of prey consumption.

Tables 8.7 and 8.8. Frequency of capture for the subjects in strain in Experiment 4c. The top table, 8.7., lists the number of captures for the strain of Captors on each test session for each treatment condition (i.e., capture followed by eat or no eat following capture) and the bottom table, 8.8., lists the frequency of capture for the strain of Non-Captors. See text for additional explanation.

CAPTORS

TREATMENT	SESSION											
	1	2	3	4	5	6	7	8	9	10	11	12
EAT (n=5)	5	4	5	4	5	5	5	4	5	4	5	5
NO EAT (n=5)	5	5	5	5	5	5	5	5	5	4	5	5

NON-CAPTORS

TREATMENT	SESSION											
	1	2	3	4	5	6	7	8	9	10	11	12
EAT (n=3)	2	2	2	3	2	1	1	2	3	.2	1	1
NO EAT (=3)	1	2	2	2	0	0	0	0	0	0	0	0
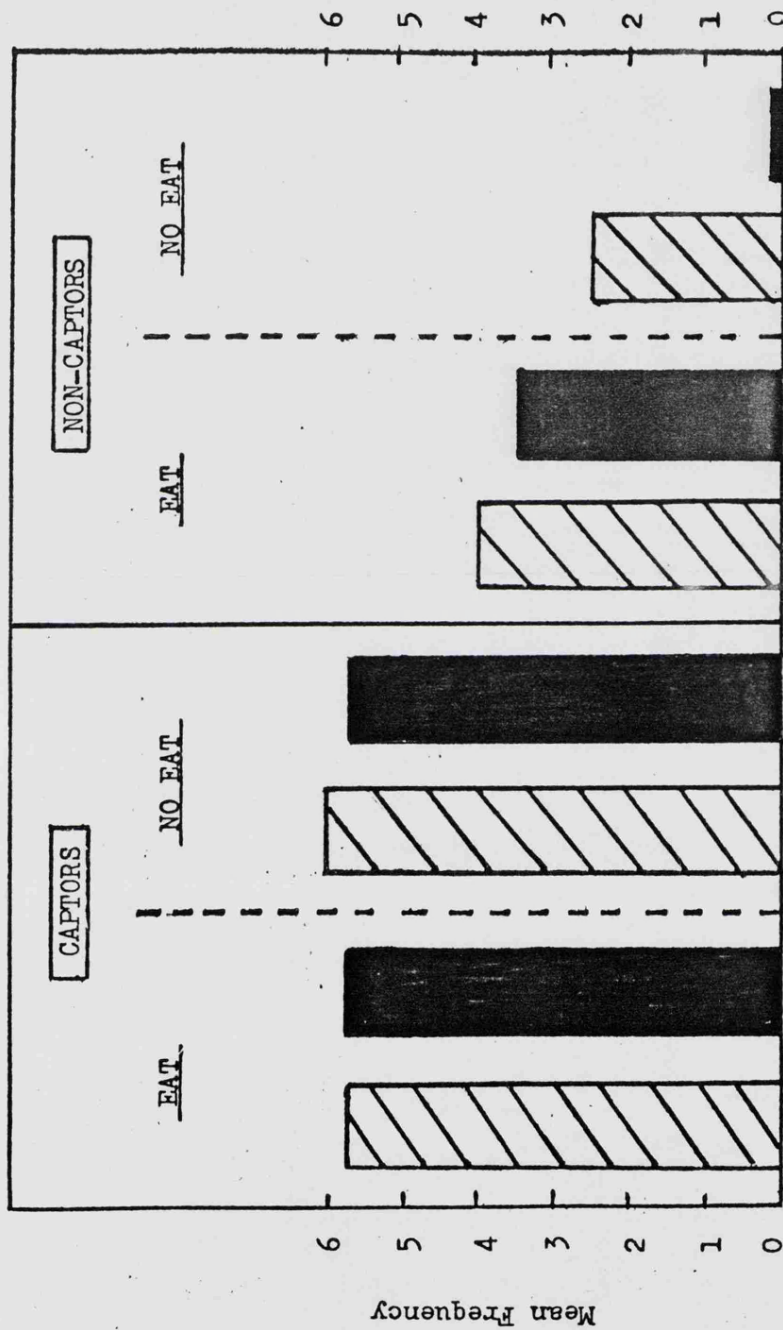
Figure 8.6. Mean number of captures for each strain under each condition in Experiment 4c. The twelve test sessions have been blocked into two successive blocks of six each. (▨ Block one; ■ Block two)

This data is summarized in the text in Tables 8.7 and 8.8.

Both tables list the total number of captors for each strain over

the 12 test sessions for each treatment condition. For example,

inspection shows that those of the Captor strain which were allowed

to eat following capture, captured on every test session with the

exception of sessions two, four, eight and ten. Those Captors

which were not allowed to eat captured with even a higher incidence;

for example, with the exception of test session ten (where four out

of five captured) every Captor captured on every test session.

The incidence of capture, however, was markedly lower for the

strain of Non-Captors, as Table 8.8 indicates. For example, of

the three Non-Captors who were allowed to eat after capture there

were only two sessions (four and nine) in which all three captured.

On most sessions only one, or two, of these subjects captured. For

the Non-Captors who were not permitted to eat the incidence of

capture was even lower. As indicated, on session one, one out of

three captured; on sessions two, three and four, two out of three,

and on sessions five to twelve no subject in this group captured.

Figure 8.6 presents these frequencies in graphical form. In

this figure the 12 test sessions have been blocked into two groups

of six each. The vertical bars represent the mean number of captures

by each strain under each condition for each test block. For example,

re-examination of Table 8.7 shows that the five Captors who were

allowed to eat made, in total, 28 captures on block two (sessions

six through twelve) for a mean frequency of 5.6. The mean for the

other three groups (e.g. Captor-No Eat; Non Captor-Eat and

Table 8.9. Comparison between the different
treatment groups of Experiment 4c in terms
of the frequency of capture over the twelve
test sessions. Test sessions have
been grouped into two successive blocks of
six. The left hand column indicates the
two groups being compared and the adjacent
columns to the right list their respective
U score for each test block as determined by
the Mann-Whitney U test. The bracketed figures
within each cell represent the mean number of
captures for each treatment group on each test
block, respectively. All probabilities are
based on two-tail tests.

	TEST BLOCK	
GROUP COMPARISON	1	2
CAPTOR - EAT vs. CAPTOR - NO EAT	(5.6) 10 (6.0)	(5.6) 12 (5.8)
CAPTOR - EAT vs. NON-CAPTOR - EAT	(5.6) 3.5 (4.0)	(5.6) 3.0 (3.3)
CAPTOR - NO EAT vs. NON-CAPTOR - NO EAT	(6.0) 0^{b} (2.3)	(5.8) 0^{b} (0)
NON-CAPTOR - EAT vs. NON-CAPTOR - NO EAT	(4.0) 2 (2.3)	(3.3) 0^{a} (0)

$^{a}p < .05$

$^{b}p < .02$

Non Captor-No Eat) were derived in a similar manner. To further

clarify this point take the case of the Non-Captors which were

denied the opportunity to eat after capture (e.g. the Non Captor-

No Eat group). These subjects made a total of seven captures on

block one (sessions one - six) for a mean frequency of 3.5; on

block two, however, no subject captured; therefore the mean

frequency was zero.

In order to determine if significance existed between the

frequencies, Mann-Whitney U tests were conducted and the results

appear in Table 8.9. The figures in brackets within each cell

represent the means as presented in Figure 8.6. Inspection shows

a lack of significance between the Captor-Eat and the Captor-No Eat

groups. In other words, those Captors who had the prey removed

after capture captured about as frequently as the Captors who were

permitted to eat. In similar fashion, no significance emerged

between the Captor-Eat and Non Captor-Eat groups. It should be

noted, however, that the frequencies were higher for the Captor-

Eat group on both test blocks. Further, inspection of this table

is most revealing, for it shows that significance existed between

the two strains for the No Eat condition. More precisely the

Captor-No Eat group made significantly more captures on both test

blocks than their counterparts in the Non-Captor group. Perhaps

of even greater interest was the fact that the Non Captor-Eat group

made significantly more captures on block two than the Non Captor-

No Eat group. Likewise, on block one the difference between the two

groups was substantial; however, it failed to reach significance at

the .05 level.

8.3c.   Discussion

Experiment 4c has demonstrated that consumption of prey

following capture is more rewarding for some subjects than others.

Specifically, the results suggest that for subjects predisposed not

to capture (to avoid the negative, one could say, for example, pre-

disposed towards avoidance or indifference, rather than 'not to

capture') eat after capture is an experience which is essential for

the development of the predatory response. As we have seen, hamsters

of the Non-Captor genotype which initially captured, but which were

always denied the opportunity to eat, eventually stopped capturing

altogether. Denying these animals the post-capture experience res-

ulted in the extinction of capture per se. This finding, then,

clearly supports the hypothesis that was outlined earlier in this

chapter.

The fact that hamsters of the Non-Captor genotype which were

allowed to eat continued to capture also adds weight to this hypoth-

esis. It should be noted, though, as Table 8.8 indicates, that the

incidence of capture for this group (i.e. Non Captor-Eat) was not as

high as one could have hypothetically hoped for. Ideally, in theory,

all hamsters that were allowed to eat after capture should have con-

tinued to capture on most occasions when subsequently tested,

regardless of genotype. This did in fact happen for the strain of

Captors, as expected.

However, for the strain of Non-Captors there was one subject

in the Eat group who failed to capture on most occasions (subject

F11; see raw data, Appendix B, Table 22). Since the sample size

was small this in turn had the effect of lowering the overall mean

(see Figure 8.6), although statistically, it did not differ signif-

icantly from the means of the Captor-Eat and Captor No-Eat groups.

Why this happened could have been due to a procedural artifact.

It may be recalled that all subjects in both strains had the prey

removed after the initial criterion capture on Day 40, 41 or 42.

This step was taken to standardize the treatment for the four

groups after the initial capture. Hopefully, it was reasoned that

a Non-Captor's tendency to capture, albeit weak, would have caused

it to attempt capture at least a second time, and with this second

capture it would have experienced eat (if a subject captured, the

prey was left in the compartment until it was consumed, or until the

next test session; no five minute time limit was imposed as in

previous experiments). This, it was thought, would have overridden

any negative effects prey removal might have had after the criterion

capture. However, it seems that for this one subject, at least, eat

after first capture was an experience that had to occur in order to

strengthen its already weak disposition to capture. Therefore,

because the prey was removed the experience needed to strengthen the

tendency to capture was, in principle, denied, and because of this

it did not come to attempt capture on the second and most subsequent

test sessions. Perhaps with a slightly different procedure (that is,

starting from the initial criterion test all subjects would have been

allowed, or denied, the opportunity to eat) subject F11 would have

continued to capture like the other two subjects in its group.

291.

In marked contrast to the above findings examination of the

capture incidence for the strain of Captors shows conclusively

that all subjects in both treatment groups continued to capture

on nearly every one of the 12 test sessions. Hence, on the basis

of this result, one can conclude that the post-capture experience

plays a negligible role in the development of capture for those

hamsters possessed with a strong disposition to capture. In short,

for these subjects, it appears that the pre-capture experience is

a self-reinforcing event.

It is also likely that hamsters with a strong disposition to

capture need relatively less pre-capture experience for the develop-

ment of this behaviour. The full-fledged capture response (i.e. a

15 second hold on the prey) developed in an exceptionally fast

manner for the ten subjects in the two Captor groups. In fact, all

of the ten subjects selected for this experiment captured within

65 seconds on Day 40. Further, nearly all captured in an extremely

efficient manner, with virtually no hesitation after the prey was

detected.   By observing this rapid development one could conceiv-

ably come away with the opinion that we were dealing with some sort

of 'innate' behaviour. Certainly the reaction of some of these

subjects fulfilled the conventional criterion needed for innate-

ness, as outlined earlier in Chapter 2 (Section 2.4b.4).

8.4   GENERAL DISCUSSION

Two paramount conclusions emerge from the three experiments
reported in this chapter. Perhaps the most significant is that the
predatory response, as a whole, can be categorized into two gross
components: an appetitive pre-capture phase and a consummatory
post-capture phase. The empirical findings support such a distinc-
tion, for they indicate that the experiences obtained within each
phase may be, to a greater or lesser degree, both important and
necessary. The second conclusion, most clearly borne out in third
experiment, and one which ties in directly with the first, suggests
that an animal's genotype determines the relative influence of the
experiences received within each phase.

The importance of these two conclusions should not be under-
estimated. Each in turn must be fully understood in order to state
which phase, the pre-capture or post-capture, is most important in
the development of locust capture. In summary, it appears for those
subjects with a weak disposition to capture, the experiences available
in both phases play a large part. In contrast, those subjects with
strong dispositions apparently only need the experience of pre-capture;
denying hamsters of this genotype the experience of post-capture seems
to have little or no effect.

Dichotomizing the predatory response into that of pre-capture and
post-capture was also desirable for practical reasons. Procedurally,
as we saw, a fairly straightforward operation separated each of these
two experiences from each other; all one had to do, for example, was

to present a dead locust, or remove a live locust immediately after capture.

Lastly, another consistent finding, but one which has not been conclusively demonstrated, concerns another effect of the post-capture experience. In addition to the beneficial effects of eating the prey _after_ a capture, Experiments 4a and 4b have shown that eating a dead prey _before_ capture also carries with it positive consequences. It is not difficult to account for this finding if one realizes that the post-capture primarily serves to strengthen the overall tendency to capture. Thus, if the tendency is strengthened, hence leading to a greater likelihood of capture, then it would seem to make little difference when eat occurred. However, it should be realized that eat after capture is more advantageous, for with this an animal also benefits simultaneously from the pre-capture experience, which as stated, is self-reinforcing in its own right.

In Chapter 9 a series of experiments are reported which attempted to deliniate the nature of the post-capture experience more fully. Primarily, the experiments set out to replicate the finding that feeding on dead prey has beneficial effects. Further, other factors are explored, such as the age of a subject at the time of dead eat, the interval between dead eat and test, and the effects of manipulating dead prey.

9

FURTHER ANALYSIS OF THE POST-CAPTURE EXPERIENCE

If the experience of eating dead prey increases the chances

of capture, then one could expect this effect to exert itself most

strongly early in an animal's ontogeny. This is so because we know

that the experiences an animal undergoes early in life often have

profound and lasting effects on later behaviour (see Chapter 2,

Section 2.4b.4a for material relevant to predatory behaviour, and

consult Sluckin, 1970, 1971 for a general treatment of this topic).

The fact that food habits, feeding preferences, etc. can be shaped.

by early food consumption has been the subject of a recent review

by Capretta, Moore and Rossiter (1973) and additional evidence

along these lines comes from Galef and associates (Galef and

Henderson, 1972; Galef and Sherry, 1973) in their studies with rats,

and Kuo (1967) in his studies with dogs. The food habits of several

non-mammalian species such as turtles and chicks have also been found

to be influenced by early feeding experiences (Burghart and Hess,

1966; Hess, 1964; Meyer and Frank, 1970; Rabinowitch, 1968). So in

view of these findings, and the results presented in the last

chapter, it seemed whorthwhile to begin further analysis of the post-

capture experience by examining what effect prior dead eat, adminis-

tered early in a hamster's ontogeny, had on later prey capture.

9.1.   EXPERIMENT 5a: THE EFFECT OF EARLY DEAD EAT

9.1a.   Design and Procedure

Subjects were derived from seven litters born between 19th

September and 15th October, 1973. On the day of birth an entire

litter was randomly assigned to one of the following treatment

conditions: <u>Group I</u>, which experienced dead eat once daily bet-

ween 5 and 14 days of age; <u>Group II</u>, which experienced dead eat

once daily between 15 and 24 days of age and, last, the <u>Control</u>

group, which experienced no dead eat prior to testing. In total,

two litters were assigned to Group I (for a total of 17 subjects;

mean litter size of 8.5), two litters to Group II (for a total of

17 subjects; mean litter size of 8.5) and three litters to the

Control group (for a total of 23 subjects; mean litter size of 7.6).

For the two experimental groups treatment consisted of deposit-

ing between eight and ten dead 5th instar locusts (killed about a

half-hour beforehand in boiling water) into the maternity cage.

Initially, for the subjects in Group I the prey was dropped directly

into the nest as near to the pups as possible. Towards the latter

part of treatment (Days 12 - 15) the prey was placed on the nest's

periphery. In addition, on most treatments for Group I (and Group

II as well) the mother was removed from the cage for approximately

ten minutes after the prey was introduced. This step was taken in

order to prevent the mother from pouching and eating the prey before

the pups had the chance to do so.

Basically the same procedures during treatment were followed

for Group II. It differed, however, in that on most occasions the

dead prey was placed in the middle of the maternity cage rather than

in the nest or on its periphery. However, on the first few occas-

ions Group II, like Group I, also had several locusts dropped into the

nest itself. In addition, on the last few treatments for both

Groups I and II several locusts were chopped up into segments rather

than presented whole (about 5). This step was taken so as to ensure

that all pups of a litter had an equal chance to feed on the prey.

Prior to weaning, pups in all three groups were provided with

greens and carrots twice a week. However, for the pups in the two

experimental groups the amount given was cut down substantially

during the ten day period in which treatment was administered.

Again this step was taken in order to increase the likelihood of the

pups feeding on the dead prey as opposed to some other food substance.

All subjects were weaned at 25 or 26 days of age, weighed, sexed

and assigned to an individual testing compartment. Subsequently,

prey capture tests were administered starting at approximately 35

days of age; tests continued once per day for three successive days

and on all active 4th instar locusts were used. Subjects were allowed

a maximum of five minutes per test to capture.

Following the last test several subjects from each group

(specifically, eight subjects from Group I, seven from Group II and

5 subjects from the Control group) who failed to capture (on all three

tests) were selected out and proffered a freshly killed 5th instar

locust on each of the two days which followed. On the day after

(the third day following the last test) these subjects were again

tested for five minutes with an active 4th instar locust.

During treatment notes were made concerning the reaction of

the pups to the dead prey. During the tests the principal measure

taken was latency to capture, and this was recorded on a stop watch.

9.1b.   Results

The mortality rate subsequent to weaning and prior to testing

was lower than the rates reported in the previous experiments. All

subjects from Group I and the Control group completed testing; two

subjects died from Group II (M6, F8), a third died after the first

test (F7) and a fourth (M5) was obviously in a poor state of health

at the commencement of testing and hence was not tested.

The behaviour of the pups in the experimental groups during

treatment was of considerable interest. For example, some pups in

both litters of Group II showed intense withdrawal upon their initial

encounter with the prey. This took the form of scrambling rapidly

out of the nest in an unorientated fashion. In marked contrast,

several pups in Group II showed no such withdrawal, but instead began

to feed on the prey shortly after it was dropped into the cage. In

fact, some subjects behaved as if they were trying to capture; i.e.

by seizing, nipping and grasping the prey (even though it was dead).

Further, on the last few treatment sessions it appeared that prey feeding was socially facilitated. For example, as stated both litters in Group II had the prey deposited in the middle of the cage on most treatment sessions. Soon after this, if the pups were in the nest one would wander out, sniff the air, locate the prey and begin to feed on it. Almost simultaneously, or shortly after, another would follow in the same manner, and within five minutes it was not unusual to find all of the pups out of the nest feeding.

For the two litters in Group I withdrawal behaviour was not as marked on the initial test session (Day 5). This could in part have been due to their poor muscular and sensory development. However it was noted that an immediate increase in restlessness occurred after the prey was dropped into the nest (i.e. the pups started squirming). Eventually, like the more pronounced withdrawal behaviour of the pups in Group II, this restlessness did wane after several treatments. On the first few treatments it was unlikely that the pups of Group I ate any prey (previous research, Dieterlen, 1959, has shown that a hamster pup does not ingest its first solid food until about eight days of age) although when treatment was administered on the following day all of the prey from the previous day's treatment was missing. It was therefore assumed that on the initial sessions the mother ate most, if not all, of the prey (after she was returned). Frequently, though, after her return the mother was seen to pouch the prey and then remove it about five minutes later; she would then deposit it on top of the nestling pups or place it on top of the food pile. Moreover, observations showed that all pups in both litters of Group I ate at least some of the
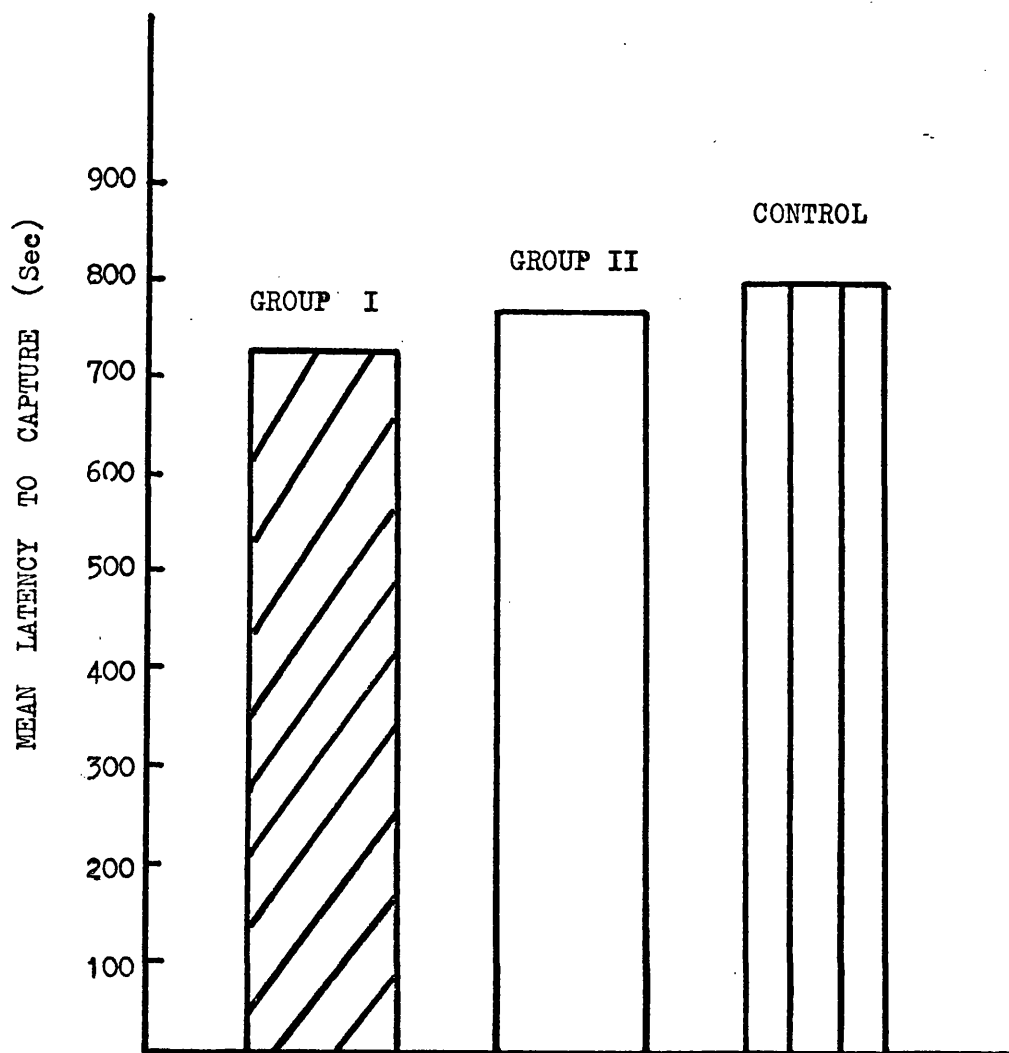
Figure 9.1. Mean latency to capture for the three
groups in Experiment 5a. Sexes and test sessions
within each group have been combined. Group I
experienced dead eat between 5 and 14 days of age;
Group II experienced dead eat between 15 and
24 days of age. The control group experienced no
dead eat prior to testing.

Table 9.3.   Probable effects of prior feeding on dead
prey. For those subjects who fail to eat, capture
is an unlikely occurrance. For those who eat the
chances of capture increase. Additional explanation
is given in Footnote 1, Chapter 9.

TEST

		CAPTURE	NO CAPTURE
TREATMENT	EAT	LIKELY	UNLIKELY
	NO EAT	UNLIKELY	LIKELY

prey on the latter (treatments 5 - 10) treatment sessions.

Raw data in terms of latency to capture for all subjects appears in Appendix B, Table 23. Inspection of this data showed that there was no gross difference between the sexes or between test sessions for any group. For this reason and for the sake of statistical brevity the sexes and sessions were combined. Thus the maximum score any subject could have obtained was 900 seconds. Graphical presentation of this data appears in Figure 9.1. As indicated, the mean latency to capture for all groups was between 700 and 800 seconds. Differences between the groups in terms of latency fell short of statistical significance as determined by the non-parametric Kruskal-Wallis test, corrected for ties (H = 4.80, df = 2, p < .10, two-tail).

Results on the re-test were also negative. That is, of the eight subjects in Group I who were allowed to feed twice subsequently on a dead locust, only three captured when re-tested; in Group II two captured (out of seven) and in the Control group one captured (out of five). Thus differences between groups were minimal.[1]

---

1. This lack of significance could stem from the failure of about half the subjects in each group to eat the dead prey on the two preceding treatment days. This failure to eat is interesting when compared with the incidence of eat in the previous experiments, where dead prey was offered. In these experiments hamsters derived from a heterogeneous stock were used and in most cases the dead prey was eaten. Further, in the experiments in Chapter 8, it is important to note that the few subjects who failed to eat during treatment rarely captured, and most, but not all, who ate during treatment captured when tested. These results are summarized in Table 9.3.

9.1c. Discussion

The results of this study contravene the belief that early

feeding on dead prey increases the chances of later capture. This

result was unexpected in light of what is known about the feeding

habits of different species and, in addition, somewhat unexpected

in light of the findings presented so far in this treatise.

Further, this result is even more baffling if one reconsiders

the behaviour of some of the subjects during the treatment phase.

As mentioned, some subjects in Group II behaved in a way typical

of one attempting to make capture. Although this observation is

noteworthy in that it buttresses the belief that hamsters as young

as 15 days may be capable of capturing (see discussion in Chapter 6),

it in no way accounts for the low incidence of capture during testing.

This negative finding may be explained in terms of the interval

which intervened between treatment and test. In the present experi-

ment it was approximately 21 days for the subjects in Group I and ten

days for Group II subjects. In the previous experiments where posi-

tive effects were found with prior dead eat (Chapter 8) the interval

between treatment and test was always one day. However, even this

explanation may be open to question, since several subjects in the

present experiment were selected out, allowed to feed on a dead

locust on two consecutive days, and then re-tested one day later.

As we know, prior dead eat in this case also had negligible effects.

This negative finding, however, could stem from the fact that exclus-

ively non-captors were used (remember only subjects who failed to

capture were selected; also see footnote 1 on page 301)

or because more than two dead feeds are necessary for the effect of

prior dead eat to manifest itself most strongly   (in Experiment 4a

subjects were allowed, in total, ten dead feeds and in Experiment 4b

twenty dead feeds). In the next experiment these factors were taken

into consideration.

9.2.   EXPERIMENT 5b.   THE INFLUENCE OF AGE AND TREATMENT -

         TEST INTERVAL.

In addition to the amount of dead prey eaten, the genotype of

the individual and the interval between treatment and test, another

variable which might have obliterated the positive effects of prior

dead eat was the age of a hamster at the time dead eat was experienced.

In the experiments reported in Chapter 8 dead eat was always adminis-

tered subsequent to weaning and between 40 and 50 days of age. Prey

capture tests were then conducted, commencing on Day 51. Now in view

of the positive findings reported in these experiments, and in view

of the negative findings of Experiment 5a, it might well be that a

hamster has to be a certain age before it can benefit from the dead

eat experience. If so then it would be an indication of a constraint

on hamster learning; that is, hamsters early in ontogeny are incapable

of forming memories for foods they have ingested. The biological sig-

nificance of such a constraint would be obscure but nevertheless it is

a possibility that should be examined.

Therefore, the experiment reported below, (5b), was designed

with all the considerations mentioned above in mind. Specifically,

the hamsters employed were derived from a heterogeneous stock

(hence, the factor of genotype was controlled); further, they were

allowed the repeated experience of dead feed at two different ages

subsequent to weaning (hence, adequate feed was assured and the age

factor scrutinized). Tests were then conducted for each group on

the day after the last feed and, in addition, for the younger age

group 21 days after the last feed (hence, the check on treatment -

test interval).

9.2a.   Design and Procedure

The subjects were 55 hamsters derived from seven litters born

between 25th November and 25th December, 1973. All were weaned at

23 or 24 days of age, matched for weight and assigned to either one

of the following groups:[2]

---

2.   Rather than randomly assigning subjects from each litter to an
      experimental group, as was done in the previous experiments,
      they were first matched in terms of weaning weight and then
      assigned on the basis of their weight. This step was taken
      so as to ensure that subjects within each experimental group
      were of an equal size (size being reflected in terms of weight).
      Some evidence that size was positively correlated with capture
      tendency was reported in the first experiment for the 30 Day
      Old subjects (see Chapter 5) and as the experimental programme
      progressed this author developed the intuitive feeling that
      larger hamsters were more likely to capture. This in fact was
      the topic of one experiment; however, this study will not be
      reported in this treatise but will be published elsewhere in
      the near future.

Early Eat - Early Test (EE - ET). Subjects in this group were

fed dead prey once daily commencing either at 25 or 26 days of age.

Treatment continued for five successive days. Subjects were then

tested for prey capture commencing on the day after their last feed

(Day 30 or 31). Those which failed to capture on the first test

were again tested on the next day and those which failed to capture

on this test were again tested for a third and final time on the

following day. Hence, subjects were tested until capture or until

three successive tests without capture.

Early Eat - Late Test (EE - LT). Treatment for subjects in

this group was identical to that administered to subjects in the

EE - ET group. However, rather than a one day interval between the

last feed and first test, a 21 day period intervened (i.e. test

commenced on Day 50 or 51). Subjects were tested once daily until

capture or until three tests without capture.

No Eat - Early Test (NE - ET). Subjects in this group exper-

ienced no dead eat prior to testing. Testing commenced for these

subjects at 30 or 31 days of age and was carried out in a manner

identical to that for the two groups mentioned above.

Late Eat - Late Test (LE - LT). Subjects in this group exper-

ienced dead eat once daily for five successive days between the ages

of 45 and 49 days or between 46 and 50 days. Subsequently, they were

then tested for prey capture commencing at either 50 or 51 days of

age. The procedures during testing were identical to those outlined

above.

Table 9.1. Design of Experiment 5b.[a]

GROUP	AGE AT DEAD FEED	AGE AT TEST COMMENCEMENT	TREATMENT TEST INTERVAL
EARLY EAT – EARLY TEST	25 – 26 – 27 – 28 –29 or 26 – 27 – 28 – 29– 30	30 or 31 days	1 day
EARLY EAT – LATE TEST	25 – 26 – 27 – 28 –29 or 26 – 27 – 28 – 29– 30	50 or 51 days	21 days
NO EAT – EARLY TEST	CONTROL	30 or 31 days	–
LATE EAT – LATE TEST	45 – 46 – 47 – 48 –49 or 46 – 47 – 48 – 49– 50	50 or 51 days	1 day
NO EAT – LATE TEST	CONTROL	50 or 51 days	–

[a]Ages are expressed in terms of days

No Eat - Late Test (NE - LT). Subjects in this group exper-

ienced no dead eat prior to testing. Testing commenced at either

Day 50 or 51 days of age and continued once daily until capture or

until three successive tests without capture.

The design of this experiment is summarized in Table 9.1.

As indicated, subjects which experienced dead feed prior to testing

did so on five successive occasions; testing then commenced either

one day or 21 days after their last feed. Subjects were then tested

once daily until capture or until three successive tests without

capture. On all tests only.active 4th instar locusts were used.

Subjects were allowed a maximum of five minutes to capture; if no

capture occurred within this time the locust was removed and the

session terminated.

Those subjects in groups EE - ET, EE - LT and LE - LT were

offered between one and three dead 5th instar locusts on·each treat-

ment day. In most cases two were offered but on the last treatment

they received only one. At the beginning of each treatment.day prey

which remained from the previous day's treatment was removed and

fresh prey put in. All prey was killed about a half-hour beforehand

by scalding to death in boiling water.

During treatment, notes were made on how many of the proffered

locusts were eaten and during the tests the only measure taken was

latency to capture and this was recorded on a stop watch.
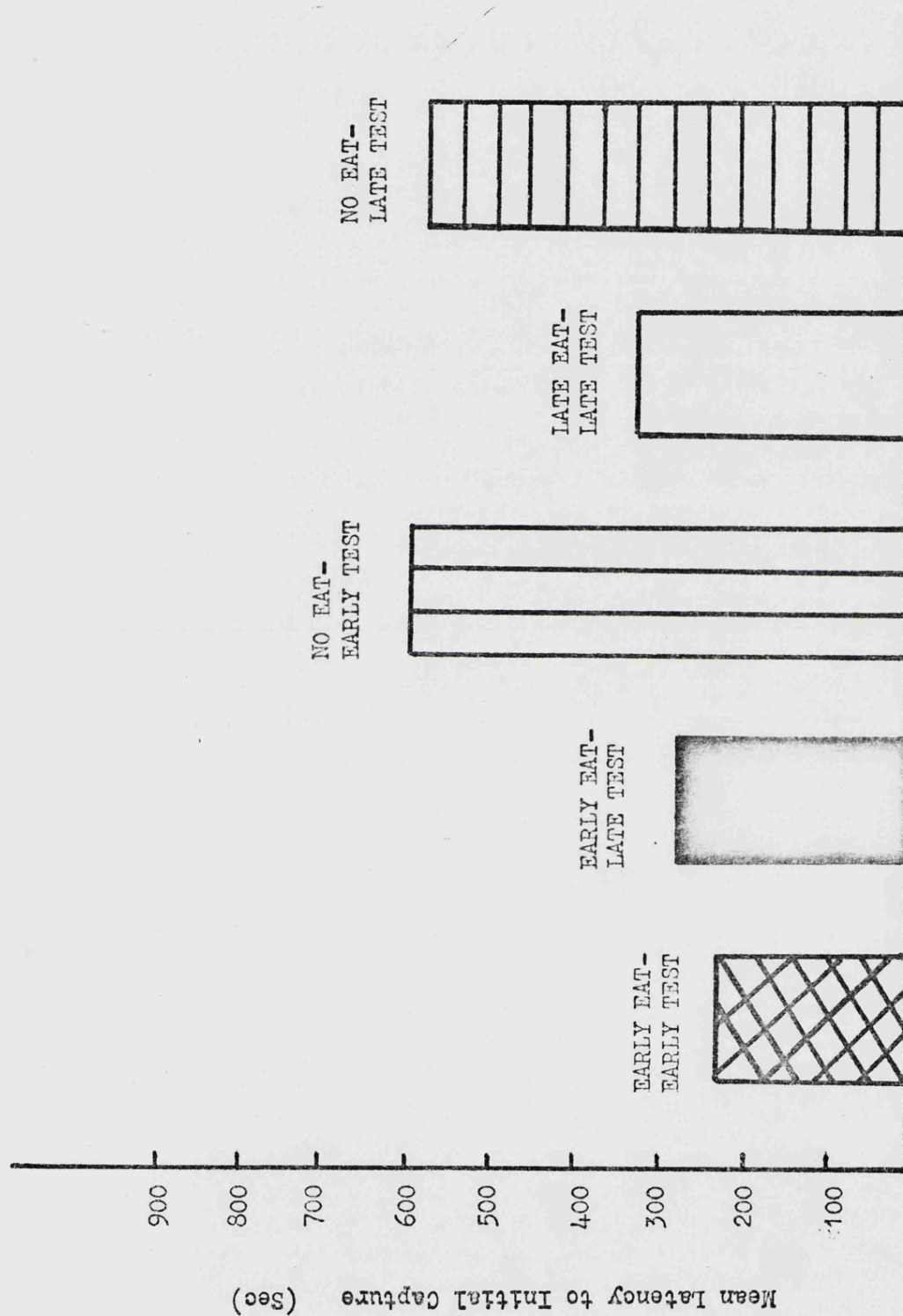
Figure 9.2. Mean latency to the initial capture for the five groups in
Experiment 5b. Sexes within each group have been combined. See text for
additional details.

Table 9.2. Summary of the analysis of variance for Experiment 5b.

SOURCE	SS	df	MS	F
Between Conditions	13476	4	3369	3.21[a]
Between Subjects	35458	10	3545	
Error	42029	40	1050	
Total	90964	54		

[a] $p < .05$ (two - tailed test)

9.2b.   Results

During treatment, prior eat subjects,(i.e. Groups EE - ET,

EE - LT and LE - LT), behaved as expected; that is to say, they

ate the proffered prey. Most eating commenced soon after the dead

prey was dropped into the compartment and in most cases all of it

was eaten. A few subjects, though, in the EE - ET group behaved

in an ambivalent manner. In other words, they reacted with both

exploration and withdrawal and in fact some even nipped. All,

however, came to eat at least some of the prey on treatment day 1

and subsequently all of it on the latter four treatment sessions.

Every subject completed testing. Raw scores in terms of

latency to the initial capture appear in Appendix B, Table 24.

Graphically, this data is presented in Figure 9.2. Examination

shows a mean capture latency of about 600 seconds for the groups that

experienced no eat prior to testing (Groups NE - ET and NE - LT).

This latency was roughly twice as great as the latencies for those

groups who experienced eat prior to testing. The overall difference

between groups was significant as determined by an analysis of

variance for matched samples. A summary of this analysis appears

in Table 9.2. Post-mortem analysis with the Ducan Multiple Range

test showed that the differences between the EE - LT and LE - LT

groups, between the NE - ET and NE - LT groups and between the

EE - ET and LE - LT groups were all negligible at the .05 level.

These findings indicate that neither the interval between treatment

and test, the age at testing nor the age at when dead eat was

experienced were variables of importance. Contrary to this,

differences between the EE - ET and NE - ET groups and differences

between the EE - LT and NE - LT groups were significant, as expected,

at the .05 level. Differences, however, between LE - LT and NE - LT

groups approached significance but did not quite reach it (specifi-

cally, the critical range value at the .05 level with the Ducan

test was 307 and the difference between these two groups was 299).

9.2c.   Discussion

The most pertinent findings of this experiment demonstrated:

1) Prior feeding on dead prey increases the chances of capture

in the naive subject.

2) Further, this experience exerts its influence in naive

animals as young as 30 days.

3) The effects of prior dead eat are lasting; that is,

the interval between treatment and test is of negligible concern.

Therefore, these findings coupled with the findings presented

in the last chapter again suggest that prior dead eat is beneficial.

How, then, can the negative results from Experiment 5a be explained?

Hamsters, it should be recalled in this experiment were fed dead

prey prior to weaning; testing then took place after an interval

of at least ten days. Further, some non-captors were selected out

following the last test, fed dead prey on two occasions and then

re-tested on the next day. As discussed, the results from both

phases of this experiment were negative; that is, it did not

increase the chances of capture. In light of these findings

Experiment 5b was designed to ascertain: 1) if an age factor

was operative (perhaps the hamsters in Experiment 5a were not old

enough to benefit from the experience and if this was the case

then it was thought that differences would have manifested themselves

between the two age groups in Experiment 5b); and 2) the import-

ance of the treatment - test interval. Moreover, an attempt was

made to control for the factors of genotype and the amount of dead

prey eaten (i.e. non-captors were not used and an adequate eat was

assured; perhaps it was these two factors which obliterated the

effects on the re-test). Thus, with these latter two factors under

control the results, as expected, were positive but somewhat sur-

prisingly the differences between the two age groups were small.

Therefore, in view of this and also in view of the fact that Experi-

ment 5b found the treatment - test interval to be relatively unimport-

ant (within the limits tested), one is simply left with the tentative

suggestion put forth earlier; namely, only post-weaning hamsters

(i.e. those 25 days and older) can benefit from the experience of

prior dead eat. This result, as discussed, might be indicative of

a constraint on learning in the hamster pup.

9.3.   EXPERIMENT 5c: DISSOCIATION OF THE POST-CAPTURE EXPERIENCE

A logical continuation of Experiment 5b would be to ascertain

the way in which the dead eat experience mediated its effect. That

is to say, what aspect of this experience was most responsible for

producing the increased tendency to capture?

Specifically, one may ask, did the experience of prior feed increase the chances of capture merely because it afforded a naive hamster the opportunity to manipulate the prey? Through manipulation a hamster could familiarize itself both visually and tactually with the size and shape of the prey as well as with its olfactory properties.

On the other hand, it is possible that the act of prey ingestion was the experience of primary importance. Through ingestion - hence familiarization through the olfactory and gustatory senses - it could be argued (as it has previously been done; see discussion in Chapter 5) that a hamster learned that what it was feeding on was in fact edible and palatable. Thus when confronted with a familiar food substance in the test situation (regardless of its shape, size or texture) capture was more likely to occur. If this was the case then it would rule out visual exposure and manipulation as the prime mediators of the prior dead eat effect.

Questions like these become relevant in view of what is known about other types of hamster behaviour. For example, in the experiment of Anton and Bennet (1972) similar questions to the ones posed above were raised. In their experiment these authors set out to train hungry hamsters to discriminate between circles and triangles in order to obtain food reward. However, before actual training began subjects were pre-exposed to the training stimuli either just visually

or both tactually and visually. In view of their past research
with rats these authors thought that those hamsters which were
visually exposed and allowed to manipulate the training stimuli
(hence exposure in the tactile sense) would perform better during
discrimination training when compared with animals which were
exposed only in the visual sense. Results, however, showed that
some exposure was better than none (i.e. compared with control
subjects who received neither visual or tactile exposure) and that
visual exposure plus tactile exposure was no more beneficial than
just visual exposure. Hence, manipulation of the training stimuli
provided no real advantage.

If prey capture in the hamster be viewed as an instrumental
means of acquiring food then it bears some resemblance to the
phenomenon under study in the Anton and Bennet experiment. The
problem for us then becomes one of experimentally dissociating all
of the potential sources of information in the post-capture experi-
ence. Thus in the experiment reported below, some animals were
allowed prior feed on a dead whole locust (i.e. one that was not
chopped up); hence, the opportunity for visual exposure, manipulation
and ingestion. Others were allowed prior dead feed on an eviscerated
locust (i.e. one that was finely chopped up); hence the opportunity
for ingestion only. Lastly, others were given the experience of just
prior visual exposure.

9.3a. Design and Procedure

40 hamsters derived from six litters born between 11th May and 14th May, 1972 served as subjects. All were weaned between 23 and 25 days of age, weighed, sexed and placed individually in a testing compartment. Subjects from each litter were randomly assigned to four groups. Each group was administered treatment between Days 30 and 39 and then subsequently tested on four occasions with the first test commencing on Day 40.

The groups to which subjects were assigned and the treatment administered were as follows:

Group 1: Cubed Locust (n = 10). Subjects in this group were visually exposed to a single live 5th instar locust inserted in a transparent perspex cube between Days 30 and 39. Exposure was continuous in that the cube was never removed from a subject's compartment except for refilling. The cube measured 1 x 1 x 1 in. and it had a removable top (sealed in place with sellotape). During treatment the cube was placed so that it rested on a compartment floor. Movement inside the cube for the locust was possible although the small size did restrict its hopping behaviour almost entirely. Moreover, the cube was not airtight; that is, small cracks were present where the sides had been glued together. However, it seemed unlikely that the cracks were sufficiently large for the odour of the prey to penetrate into a compartment. A fresh locust was put into each cube on every other day during treatment.

Group 2: <u>Eviscerated Locust</u> (n = 10). Subjects in this group were fed a single eviscerated 5th instar locust once daily between the ages of 30 and 39 days. The eviscerated prey had been killed by scalding it to death with boiling water about a half-hour beforehand (the procedure was similar to the one described previously in Experiment 4a) and then chopped up finely with scissors. During each treatment all parts of the eviscerated locust were dropped together to the compartment bottom; they were not scattered.

Group 3: <u>Dead Whole Locust</u> (n = 10). Subjects in this group were treated in a manner identical to that of Group 2 except that a dead intact locust was presented on each treatment day rather than an eviscerated one.

Group 4: <u>Control Group</u> (n = 10). Subjects in this group received neither visual exposure nor dead feed prior to testing.

Testing commenced for all subjects on the day after the last treatment and continued once every day for four successive days. All tests were carried out with an active 4th instar locust and on each subjects were allowed a maximum of five minutes to capture. The principal measure taken was latency to capture and this was recorded on a stop watch.

9.3b.   Results

All 40 subjects completed testing. Raw data in terms of latency
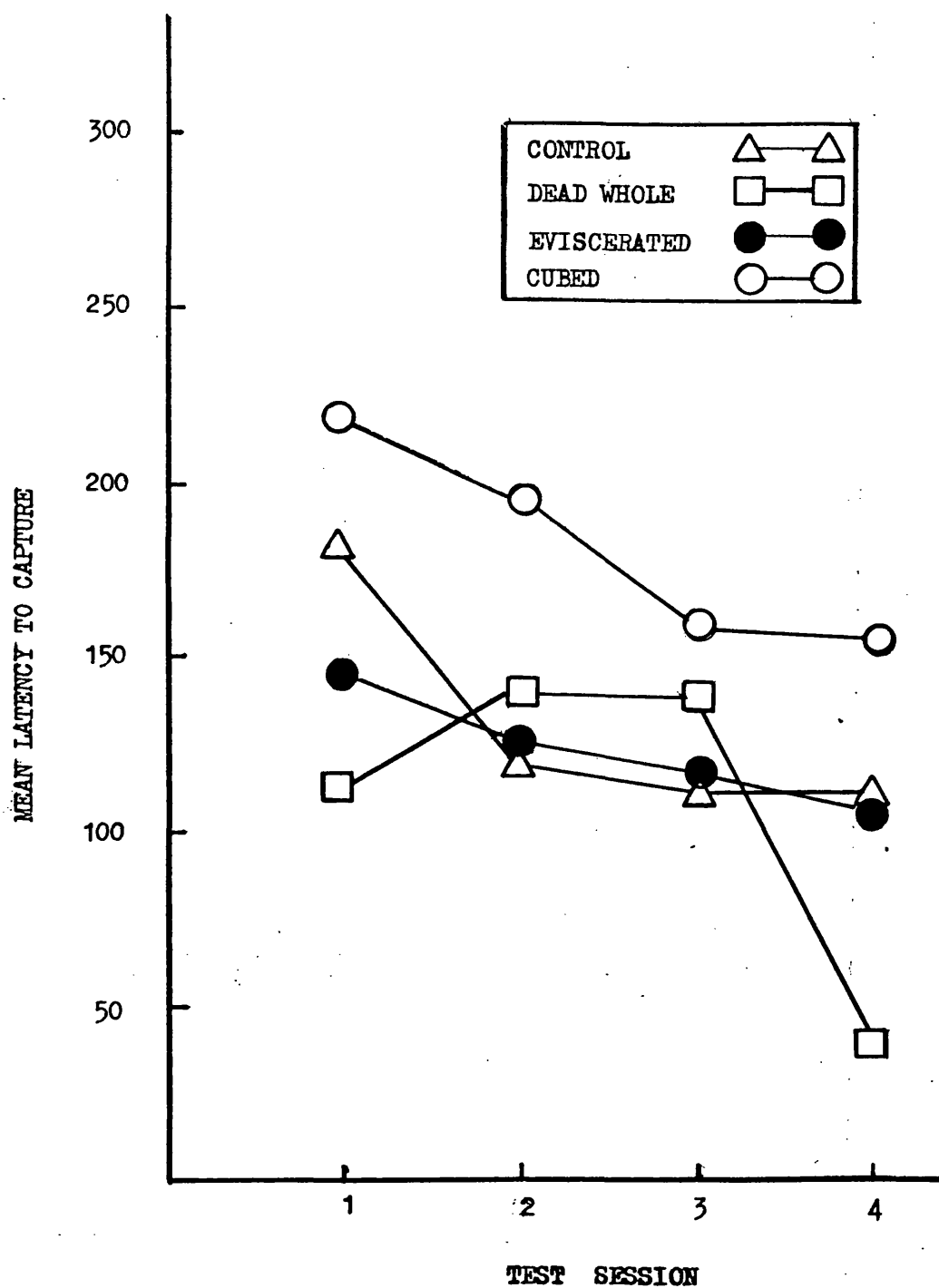
Figure 9.3. Mean latency to capture for the four groups in Experiment 5c. Sexes within each groups have been combined. See text for further details.

to capture over the four test sessions for each group appears in

Appendix B, Table 25. Graphical presentation of this data is in

Figure 9.3. The non-parametric Kruskal-Wallis test, corrected for

ties, was employed to test for significance on each session and

the results were as follows: Session 1, H = 5.29, p< .20;

Session 2, H = 1.81, p< .70; Session 3, H = .61, p< .90;

Session 4, H = 4.21, p< .30.

Chi square values were also calculated to see if the incidence

of capture among the groups differed significantly on any session.

The results again were entirely negative. Where differences might

appear to reach significance (sessions 1 and 4) actual significance

was not achieved (Session 1, x^2 = 4.14, df = 3, p< .30; Session 4

x^2 = 6.35, df = 3, p < .10).

In order to show that eat prior to test has some significant

effect (regardless if it be eviscerated or dead whole) the latency

scores for the Eviscerated group and Dead Whole group were combined

and compared to the combined latencies of the Control group and

Cubed group on each test session. One-tail t test analysis revealed

the following: Session 1, t = 2.19, df = 38, p <.025; Session 2,

t = .65, df = 38, p < .30; Session 3, t = .29, df = 38, p < .40;

Session 4, t = 1.64, df = 38, p <.10.

9.3c. Discussion

The negative results of this experiment are noteworthy in that

they pinpoint the main source of information available to a hamster during the post-capture experience. Hence, we now know that what the naive hamster ingests and not what it visually experiences (as found in the Cubed condition) or manipulates (an experience available for Dead Whole subjects) is the factor of prime importance.

If visual experience and/or manipulatory experience were important then one would have expected subjects in the Cubed (Group 1) and Dead Whole (Group 3) groups capturing with shorter latencies than subjects in the Eviscerated group (Group 2). However, differences between the Cubed and Eviscerated conditions were large (see Figure 9.3), thus indicating, if anything, that visual exposure was relatively unimportant. Moreover, differences between the Eviscerated and Dead Whole groups were negligible (on most test sessions) and when combined significantly shorter (on session 1 and nearly on session 4) than the combined latencies of the Cubed and Control subjects. Together, these latter two findings again indicate that prior eat is beneficial, and that with the experience of dead eat it is ingestion and not manipulation which plays the key role in mediating the effect.

Hamsters which ate dead prey prior to testing probably lost their fear of the prey through these eats. Therefore during the tests with live prey capture was more likely to occur. In a sense then for these prior eat subjects the post-capture experience functioned in a way normally reserved for the pre-capture experience (i.e. as theorized the pre-capture experience serves to habituate

fear). However, it would be difficult to pinpoint the modality

through which the habituation acted (see discussion below).

Further, it is of interest to note that dead eat subjects

often reacted with withdrawal on the initial tests. This was

especially true if a locust happened to hop just at the time when

a hamster was approaching and/or exploring. On the other hand, if

a locust remained motionless at the time of approach or explore,

then it appeared to be treated (by the hamster) as if it were dead

prey. That is, a hamster usually seized it with its mouth; this

was then followed by grasp and immediate feed. These observations

suggest that a hamster is capable of differentiating between moving

and non-moving prey.

Lastly, although the effect of prior dead eat is mediated

largely through ingestion it is probable that olfactory and gusta-

tory familiarization also played a role. It must be assumed that

when a hamster ingested dead prey (whether it be whole or eviscerated)

it familiarized itself with the taste of the prey as well as with its

smell. Unfortunately, the design of this experiment did not separate

out olfaction and taste from ingestion per se, or olfaction and taste

from each other. This was mainly because of procedural difficulties.

That is, how would it have been possible to allow a hamster to taste

the prey without allowing it to feed or smell, or, alternatively,

allowing it to feed without allowing it to taste or smell? Rendering

a subject anosmic through zinc sulphate treatment might be one answer

(see discussion in Chapter 2) but short of this the problem seems

insuperable. Because of these difficulties and for the sake of simplicity it would seemingly be most convenient to lump the gustatory and olfactory experience with ingestion per se and label it grossly as the experience of ingestion, realizing that it involves both taste and ingestion.

It would be prudent to argue along similar lines for the eat which occurs after capture. That is to say, possibly it was the taste and/or the smell of the locust, rather than ingestion, which strengthened the tendency to capture. But as we clearly saw in the experiment (Experiment 4c, Chapter 8) in which the prey was removed after capture, capture did become extinguished in hamsters of the Non-Captor genotype even though they were allowed quite an adequate taste. That is, there was a five second hold before the locust was removed, and it would seem that this would have been enough time for taste (and possibly smell) to occur - but not eat. On the contrary, for the Captors in Experiment 4c it is possible that it was just taste and not ingestion which served to strengthen the tendency to capture. Thus, if this be the case, one could argue that taste along with the self-reinforcing effects of the act of capture were the key variables operating in strengthening the predatory tendencies of those hamsters possessed with a disposition to capture.

9.4. GENERAL DISCUSSION

It has been demonstrated that for the naive subject, prior feed on dead prey increases the chances of capture when confronted with

live prey. Further, it has been shown that ingestion and not manip-
ulation or visual exposure is the prime mediator of this effect and
it also has been shown that the interval between dead eat and test
is of minor importance.

In addition, it should be kept in mind so as to avoid confusion,
that through experimental manipulation the post-capture experience
may occur either before or after capture. In Chapter 8 we were mainly
concerned with the eat which occurred after capture, and in this one,
Chapter 9, the chief concern was with the eat which occurred before
capture. Moreover, the experience gained and the effects produced
(i.e. increased capture tendency) from both eat before and eat after
seem to be roughly the same. It is likely, though, that prior eat
for the naive subject also acted, in part, to habituate fear of novel
live prey and this, as was hypothesized earlier, is an effect normally
reserved for the pre-capture experience.

This belief that the experience of eat before capture does not
differ radically from the experience of eat after capture rests on
the assumption that consumption of freshly killed prey does not
differ from consumption of captured prey. Perhaps one might say
that scalding the locusts to death altered some of their basic
features, especially the olfactory ones; that is, those the
Experimenter could not readily detect. This could be true, but
observations suggested that this was not the case. For example,
hamsters that did eat seemed to feed on both captured prey and dead
prey with equal vigour. In most cases all of it (i.e. the dead

prey) was eaten and further eating usually commenced in the same direction as was the case with captured prey (i.e. from the head down).

Another point one should keep in mind concerns the pre-capture behaviour of the prior eat subjects (whether it be with a dead whole locust or an eviscerated locust) when confronted with live prey in the test situation for the first time. Assumedly, if prior eat increased the tendency to capture (or more precisely stated, the tendency to engage in those behaviours which lead to capture) then one would expect those animals which experienced eat after capture to be more efficient captors (in terms of explorations needed, nips and unsuccessful captures on the first few test sessions) than those animals which experienced eat before capture. This is so, because those animals which ate before attempting capture never experienced those behaviours which have been collectively referred to as pre-capture, and it should be remembered that it is the practice which the pre-capture experience provides which in turn results in perfection and greater efficiency. No measures of pre-capture behaviour during testing were taken in two of the three experiments reported in this chapter; hence data is lacking to test this contention. This could not be done because of the lack of suitable groups for comparison; that is, most only experienced some form of post-capture. Comparisons with those who experienced the pre-capture phase would be needed. However, comparisons of this kind were made in Experiment 4a (Chapter 8) and the reader should refer back to Table 8.3 and Figure 8.3 for the results. On the whole these results, along with the

latency data (see Table 8.2 or Figure 8.2), are suggestive of the fact that the tendency to capture was strengthened without allowing perfection of the behaviours needed for capture. The increased tendency is reflected in the latencies to capture on blocks two and three (which were almost identical to those of the Capture group; that is, those who were allowed both the pre-capture and post-capture experiences) and the relative inefficiency of post-capture subjects is reflected in their relatively high rate of exploration, nip and unsuccessful capture when compared with either Pre-Capture or Capture subjects.

In Experiment 4b differences in the frequency of pre-capture behaviours between Post-Capture subjects and subjects in the Pre-Post and Capture groups were not as large (refer back to Table 8.6) although there was a definite trend for a greater frequency on all the pre-capture behaviours for the Post-Capture subjects. Perhaps the large differences which would have been expected, according to our theory, were obviated because of the unusually large dose of treatment (i.e. Post-Capture subjects were allowed to feed on twenty dead locusts rather than ten as in Experiment 4a).

10

SENSORY PRE-EXPOSURE

Having now made a fairly detailed analysis of the post-capture experience, the experience which precedes this, that of pre-capture, will be more closely scrutinized in the two experiments reported in this chapter.

To briefly review, for the purpose of emphasis, the evidence presented so far suggests that the experience of pre-capture affects the ontogeny of the predatory response in two principal ways. First, as we said, it allows a naive hamster's fear response to habituate and, secondly, it affords a hamster the opportunity to practice those behaviours needed for capture. Thus, through the pre-capture experience a hamster learns: 1) not to fear the locust, and 2) to perfect the prey capture technique.

Further, in most hamsters derived from a heterogeneous stock both of these experiences probably play some part in the acquisition of the behaviour. However, it is essential to realize that the importance of each may vary with the genotype of the individual. We know from Experiment 4c (Chapter 8) that this is certainly the case for the post-capture experience, and it is conceivable that it could hold for the pre-capture experience as well. For example, it

could be that hamsters with a weak disposition (to capture) need relatively more exposure to the prey before their fear response habituates and likewise need more practice before the prey-capture technique is developed most efficiently.

Observations from the previous experiments support this belief. For example, in Experiment 1 large individual differences between subjects in terms of frequency of pre-capture behaviours were found. Some subjects became highly skilled captors with relatively little practice (i.e. in terms of the frequency of exploration, nip and unsuccessful capture) while, on the other hand, others nipped, explored and captured unsuccessfully at relatively high rates before making their first successful capture. Moreover, in terms of the habituation of the fear response as reflected in the frequency of withdrawal behaviour, large individual differences were also manifested. For instance, at one extreme, there were subjects who captured soon after the prey was introduced with virtually no withdrawal; at the other extreme there were those which frequently withdrew without ever attempting capture on most test sessions.

Further, an important finding came forth from Experiment 2 in that it showed most hamsters would capture if given a sufficiently long test (this result has been replicated subsequently in other experiments by this author). The interpretation given to this finding, as discussed in Chapter 6, was that the increased length of the test acted on the first type of experience within the pre-capture phase; that is, the lengthy session of forced exposure effectively allowed

the fear response of most hamsters to habituate. And it was argued, with the attenuation of the fear response, most hamsters came to behave in the way typical of their species; i.e. by attempting capture.

Hence, the questions raised by this latter finding are similar in scope to those posed in the last experiment of the preceding chapter (Experiment 5c); namely, what stimulus characteristics of the prey are most important in bringing about the attenuation of the fear response? One could rephrase this question by asking what features of the prey are most novel and hence most fearful, or to what stimuli (from the prey) does a hamster have to habituate before it can attempt capture?

Two possibilities are likely: either the smell of the prey or the sight of the prey. Habituation in the olfactory sense is obviously one possibility, for it is well-known that hamsters are a macrosomatic species (refer to Chapter 3 for relevant references). Vision too could play some part for hamsters are known to have pigmented irises (Anton and Bennett, 1972); hence relatively good vision for a rodent species. In addition, other researchers have shown that vision controls other types of hamster behaviour (e.g. agonistic behaviour; see Grant, Mackintosh and Lerwill, 1970).

In the experiments reported below these possibilities will be examined. Naive hamsters, in the first experiment, derived from a heterogeneous stock, were pre-exposed (in the sense that they were exposed to the prey without allowing the opportunity to capture) either

just visually or both in the visual and olfactory modalities. In

the second experiment such factors as the age of a hamster at the

time of exposure and the interval between pre-exposure and test

were examined.

10.1.   EXPERIMENT 6a: THE RELATIVE IMPORTANCE OF OLFACTION AND

VISION

10.1a.   Design and Procedure

The subjects were 42 hamsters derived from five litters born

between 27th July and 1st August, 1973. Subjects were weaned

between 21 and 25 days of age, weighed, sexed and randomly assigned

to one of three groups. The two experimental groups were referred to

as: 1) the Perforated Cube group and 2) the Solid Cube group, respec-

tively. The control group was referred to as the Empty-Cube group.

Immediately after weaning the 14 subjects assigned to the

Perforated group were placed individually in a testing compartment

which contained a single transparent perspex perforated cube filled

with four to six active locusts. The locusts within each cube con-

sisted of nymphs of at least the 5th instar and adults without wings.

The wings of the adults were clipped in order to keep them as physic-

ally similar to the nymphs as possible; i.e. nymphs of Locusta migra-

toria do not have distinguishable wings. The cube itself rested on

the compartment floor and could be easily moved by a subject. Fresh

locusts were put into the cube every other day during treatment.
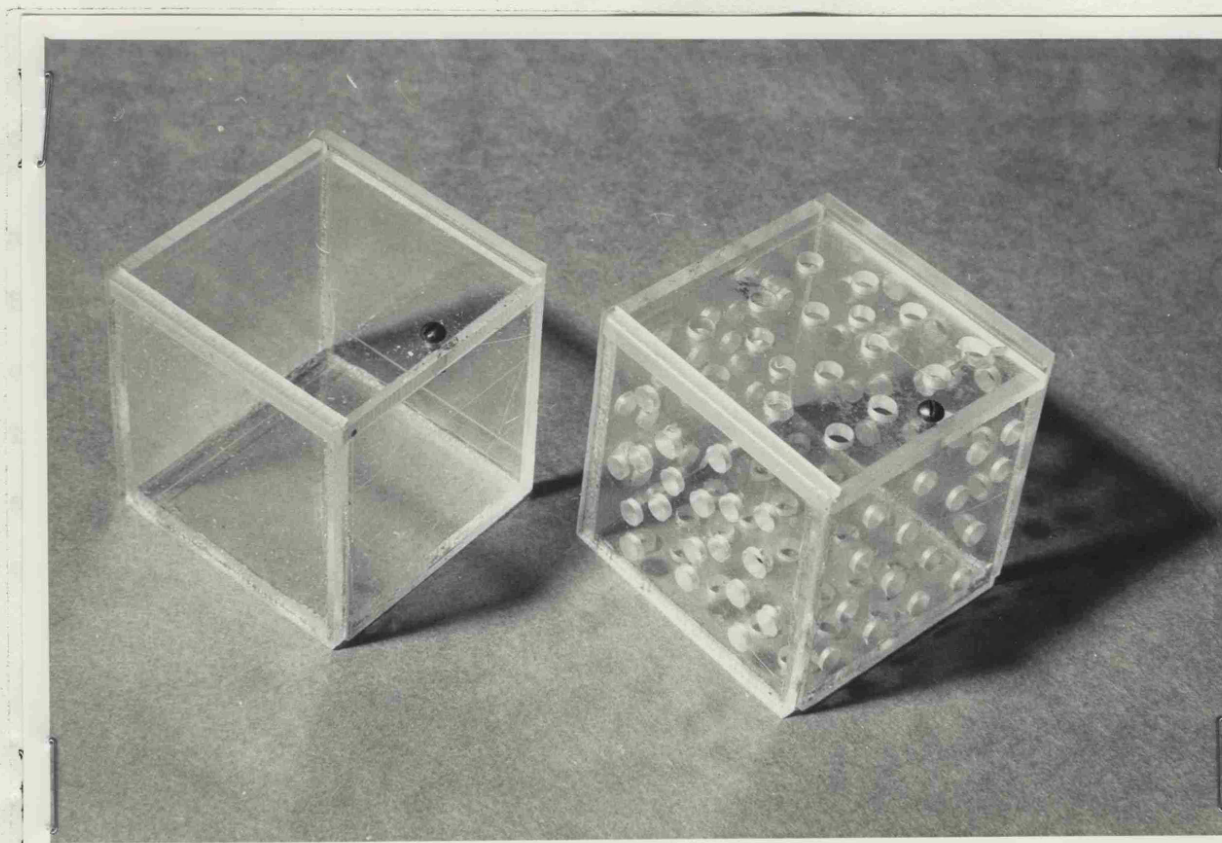
Figure 10.1. Photograph of the two types of cube used in Experiment 6a. The cube pictured on the left is the solid type and the one on the right is perforated. See text for details of their construction and dimensions.

Occasionally during treatment if a cube became dirty or foggy from

the secretions of the locust it was removed from the compartment,

washed with soap and water, dried, refilled with fresh locusts and

then re-inserted. When a cube was removed from a compartment, either

for refilling or cleansing, it was always replaced within five

minutes.

Hamsters in the Solid group and Empty group were treated in

exactly the same manner, except subjects in the Solid group (n = 14)

had no holes in their cubes (but had locusts) and subjects in the

Empty group (n = 14) had either a perforated or solid cube but with-

out locusts (half had a solid cube and half had a perforated cube).

Thus subjects in the Solid group were pre-exposed only in the visual

sense and subjects in the Empty group received neither visual nor

olfactory pre-exposure.

In order to control for the effects removing a cube from a

compartment might have had (the Experimenter accomplished this by

inserting his hand into a compartment) subjects in the Empty group

also had their cube removed every other day and occasionally it was

washed.

A photograph of a solid cube and a perforated cube appear in

Figure 10.1. All were hand-made by the Experimenter and constructed

of 1/8 in. thick transparent perspex. Each cube measured approxim-

ately 2 x 2 x 2 in. Perforated cubes differed from solid cubes in

that the former contained approximately sixteen 3/16 in. diameter

holes on each of the six sides. The sides of all cubes were made to fit as flush as possible and were glued together with a transparent cement. In order to assure that the solid cubes were airtight the inside edges where any two sides joined were covered with sellotape. Both the perforated and solid cubes had one removable sliding lid which, as shown, was held in place by a small screw.

Subjects in the three treatment groups lived with their cubes continuously from weaning until the completion of testing. Testing for all subjects commenced at 40 or 41 days of age and was carried out over two successive days (ITI of 1 day). Subjects were tested once per day; hence, in total, they were tested on two occasions. Tests were carried out with active 4th instar locusts and subjects were allowed a maximum of five minutes to capture. If a subject captured it was then allowed an unlimited time to feed on the prey. If during a test a cube happened to be up against the compartment wall, and if a locust happened to hop between it and the wall, it (the locust) was gently prodded from behind the cube with the end of a pencil. The measures recorded via a multiple pen recorder were latency to capture and the frequency of exploration, withdrawal, nip and unsuccessful capture. Tests were timed with a stop watch. Throughout the entire course of the experiment subjects had ad lib access to food and water.
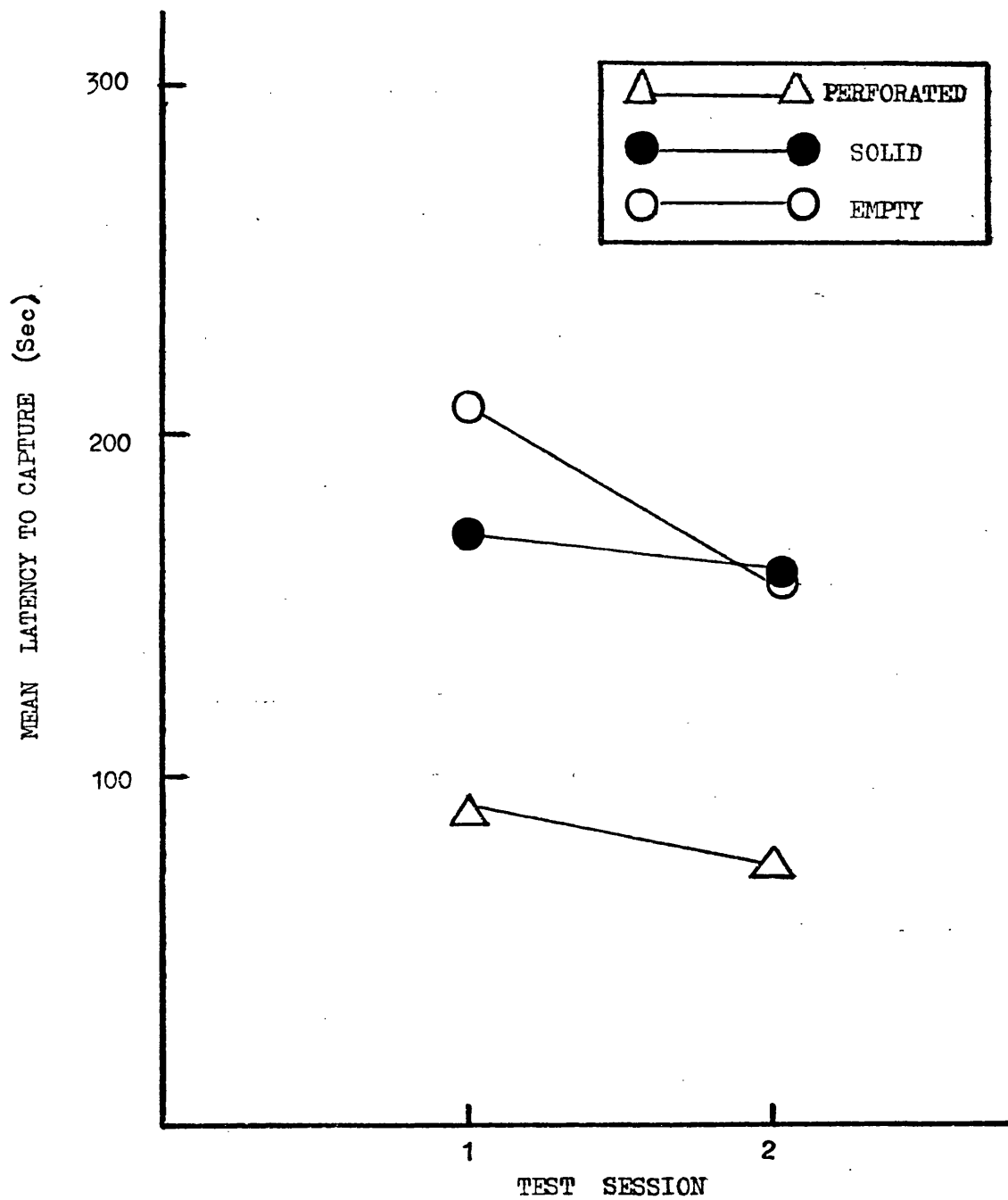
Figure 10.2. Mean latency to capture for the three groups in Experiment 6a. Males and females within each group have been combined. See text for further details.

10.1b. Results

During the course of treatment one subject from the Perforated

Cube group died (M6) and one subject from the Empty Cube group

escaped from its compartment (F5). This latter subject, although

captured by the Experimenter two days later and subsequently tested

(latencies to capture for this subject were 300 seconds on both test

sessions), was discarded from the experiment. In total, 13 subjects

from the Perforated group and Empty group, and 14 subjects from the

Solid group completed testing.

Raw data for this experiment appears in Appendix B, Table 26

for latency to capture and Tables 27, 28, 29 and 30 for the frequency

of exploration, withdrawal, nip and unsuccessful capture, respectively.

Turning first to the latency data, which is presented graphically

in Figure 10.2, inspection shows that the mean latencies to capture

were about the same on both test sessions (i.e. between sessions one

and two) for the Perforated group.   One-tail Sign tests

showed that the probability of obtaining these two values by chance

for the Perforated group was .19 (specifically, N = 12, $X \leq 4$,

p = .19) and for the Solid group it was .63 (N = 8, $X \leq 4$, p = .63).

On the other hand, for the Empty group, differences between the two

test sessions were highly significant (N = 7, X = 0, p = .008).

Two-tail Mann-Whitney U-tests were then conducted to determine

if significance existed between the groups on either Session one or

TEST SESSION
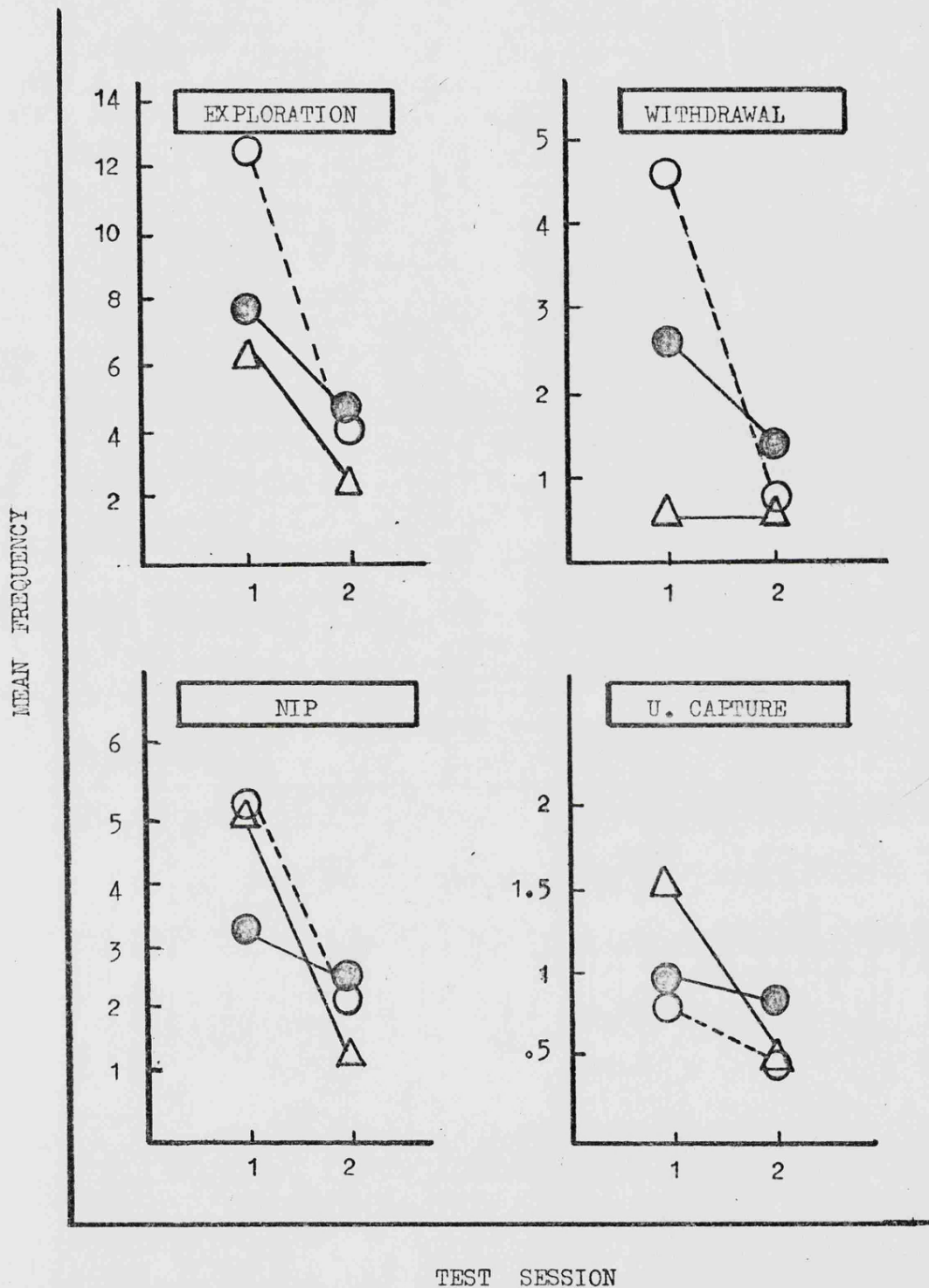
Figure 10.3. Mean frequency of exploration, withdrawal, nip, and unsuccessful capture for the three groups in Experiment 6a. Frequency scores for exploration and withdrawal are based on the scores of all subjects within each group. Frequencies for nip and unsuccessful capture are based on the scores of those subjects who captured on at least one occassion. Males and females within each group have been combined. See text for further explanation (△——△ Perforated, ◯——● Solid, ◯-----◯ Empty).

two. On Session one the results showed that the Perforated group differed significantly from the Empty group (U = 31, p < .01) but not from the Solid group (U = 72, p > .10). Differences between the Solid and Empty groups also failed to reach significance (U = 93.5, p > .10). On Session two the Perforated group again differed significantly from the Empty group (U = 40.5, p < .05); differences between the Perforated group and Solid group (U = 59.5, p > .10) and between Solid group and Empty group (U = 73, p > .10) fell short of significance.

The mean frequency of the other behaviours recorded in this experiment appear in Figure 10.3. Looking first at the exploration data, inspection shows a decrease in the frequency of exploration for all groups on Session two. One-tail Sign tests indicated that the difference between sessions one and two was significant for the Perforated group (N = 13, X $\leq$ 2, p = .01) and for the Empty group (N = 13, X $\leq$ 2, p = .01) but not for the Solid group (N = 12, X $\leq$ 3, p = .07).

Significant differences between groups were also manifested in several instances for the exploration data. For example, two-tail Mann-Whitney U tests revealed that the Empty group explored significantly more on Session one than the Perforated group (U = 29, p < .01). Likewise, the difference between the Solid and Empty groups was significant (U = 50, p = .05). However, no significance existed between the Solid and Perforated groups on Session one (U = 66.5, p > .10). On Session two the groups did not differ significantly from one another,

although as Figure 10.3 indicates, the Solid and Empty groups

explored considerably more often than the Perforated group.

As was the case for the exploration data, the Empty and Solid

groups also had fewer withdrawals on Session two than on one. For

the Perforated group the frequencies were about the same (mean of

.6 for Session one and .5 for Session two). One-tail Sign tests

showed that the difference in the frequency of withdrawal between

sessions was highly significant for the Empty group ($N = 10$, $X \leq 0$,

$p = .001$) but not for the Solid group ($N = 8$, $X \leq 2$, $p = .14$) or

Perforated group ($N = 5$, $X \leq 2$, $p = .50$). In terms of the difference

between groups on each test session (for withdrawal behaviour) the

only significance to emerge was on Session one between the Perforated

and Empty groups ($U = 33$, $p \leq .01$, two-tail).

Analysis of the frequency data for nip and unsuccessful capture

was made on the scores of only those subjects who captured on at

least one occasion. Exclusion of the non-captors was justified because

they rarely nipped or attempted capture. In total, 12 subjects from

the Perforated group, 8 subjects from the Solid group and 7 subjects

from the Empty group fulfilled the criterion of capture on at least

one occasion in the two times they were tested. Examination of

Figure 10.3 shows that all groups made fewer nips and unsuccessful

captures on session two than on one. For nip, the decrease was

significant for the Perforated group ($N = 11$, $X = 0$, $p = .006$, one-

tail Sign test) but not for the Solid group or Empty group ($N = 7$,

$X \leq 3$, $p = .50$ for the Solid group; $N = 7$, $X \leq 2$, $p = .22$ for the

Empty group). For unsuccessful capture the difference between

sessions was significant for the Perforated group (N = 9, $X \leq 1$,

p = .02, one-tail Sign test); significance, however, was not

achieved for the Solid group (N = 6, $X \leq 3$, p = .65) or Empty group

(n = 4, $X \leq 1$, p = .25).

10.1c. Discussion

The results of Experiment 6a suggest the following:

1) The experience of pre-capture serves to increase the
chances of capture in the naive hamster.

2) Pre-exposure in the olfactory sense seems to be the
principal sense modality through which this experience operates.
Solely visual pre-exposure may have a beneficial effect, but on its
own it does not seem to be as essential as olfactory pre-exposure.

3) Pre-exposure, as part of the pre-capture experience, acts
primarily to reduce a naive hamster's fear of the locust; it does
not seem to act on the second type of experience within the pre-
capture phase - i.e. perfecting the behaviours needed for capture.

Point one above is straightforward. The increased likelihood
of capture was best reflected in terms of latency to capture; that
is, pre-exposed hamsters of the Perforated group captured with a sig-
nificantly shorter latency than non-pre-exposed hamsters of the Empty

group, both on Session one (p< .01) and Session two (p <.05).

On the other hand, hamsters which were just visually pre-exposed (e.g. subjects in the Solid group) did not differ significantly from subjects which received both olfactory and visual pre-exposure (Perforated subjects) or no pre-exposure (Empty subjects). However, it would be fair to note that when compared with the latencies of Perforated subjects, latencies for Solid subjects were considerably higher on both test sessions (for the Solid group means of 175.9 and 166.3 for sessions one and two, respectively; for the Perforated group means of 94.2 and 84.0 for sessions one and two, respectively). Further, the mean latencies for the Solid group were somewhat lower than the latencies for the Empty group (but not significantly different - see Figure 10.2). Therefore, by making all possible latency comparisons (e.g. between the Solid and Empty, Solid and Perforated and Perforated and Empty) one gets the impression that visual exposure on its own may have had a small positive effect (thus resulting in a marginal increase in the likelihood of capture for the subjects in the Solid group).

As noted earlier, it is known that hamsters have pigmented irises (Anton and Bennet, 1972); hence relatively good vision. Therefore, one could reasonably attribute some weight to this latter hypothesis. In the Anton and Bennett experiment, hamsters were pre-exposed visually much in the same manner as they were in the present experiment; that is, by inserting the appropriate stimulus object into a container into which they could see. The results of their experiment showed

this treatment had beneficial effects on the behaviour in question
(i.e. discrimination training in which subjects had to jump from a
platform) in the test situation.

Moreover, one could argue that the lack of a more pronounced
effect from solely visual pre-exposure might have been due to the
fact that hamsters simply could not visually perceive the prey
during the red phase of the reversed day - night cycle. This,
however, seems unlikely. As noted in Chapter 4, illumination into
each compartment during the red phase was moderately bright, and
it is also probable that it contained some white light (pure red
light is difficult to obtain in the red bulbs bought commercially).
Further, if this was not the case, then it could be argued that a
hamster still had adequate opportunity for visual exposure during
the white phase of the light cycle (about 15 hours daily).

In conclusion, then, olfaction definitely seems to be one
mediator of the pre-exposure effect, with the role of vision ques-
tionable, but possibly having some influence., In the present
experiment, the fact that Perforated subjects had both visual and
olfactory pre-exposure confounds the issue in that these subjects
were pre-exposed in two modalities simultaneously. Possibly a
clearer picture would have emerged if a fourth group was included
which was pre-exposed only in the olfactory modality. This could
have been easily accomplished by coating the inside of a perforated
cube with black paint, or something similar. Such a group would have
been effectively pre-exposed only in the olfactory sense, and their

latencies could have therefore been more meaningfully compared with subjects which received only visual pre-exposure, or visual and olfactory pre-exposure, or no pre-exposure whatsoever.

The third finding of importance to emerge from this study concerns the consequences of pre-exposure. Re-examination of Figure 10.3 should help clarify this point. Inspection shows that on session one subjects in the Perforated group explored less ($p < .02$) and withdrew less ($p < .02$) than subjects in the Empty group. On the other hand, the frequency of nip was roughly the same and the unsuccessful capture rate was nearly twice as great (however, not significantly different, $p > .10$). The fact that exploration and withdrawal were significantly lower on session one for the Perforated group suggests that pre-exposure familiarizes Perforated subjects with the novel prey, hence helps reduce their fear and therefore increases the chances of capture. Thus, in light of this finding it is probable that the experience of pre-exposure, as it occurred in the present experiment, simulated and fulfilled the first function of the pre-capture experience; namely, that of fear reduction.

The second function of the pre-capture experience, that of enabling a hamster to practice those behaviours needed for capture, was an experience which pre-exposure could not provide. The results concerning the frequency of nip and unsuccessful capture bear this point out most clearly. As indicated (see Figure 10.3), the difference in frequency between groups for each of these behaviours was

not as great as it was for exploration and withdrawal. If pre-
exposure exerted an influence on nip and unsuccessful capture then
one would have expected the frequencies for the Perforated group
to be lower. However, if anything, they were higher, and this can
be accounted for simply by realizing that pre-exposure had little
influence on those behaviours needed for capture.

A final point to note is the decrease in frequency for most
behaviours on session two. Likewise, the latency data for the
Empty group also decreased significantly from Session one to Session
two. These findings are consonant with the findings reported in the
earlier chapters, and as before the decrease may be accounted for
in terms of the experience gained in the test situation itself,
(the reader should refer to Chapter 2, Section 2.4b.4b. if there is
any doubt as to what is meant by "in the test situation"). It is
interesting to note, though, the lack of decrease in withdrawal
behaviour between sessions for subjects in the Perforated group.
That is, hamsters in this group showed a low incidence of withdrawal
on both sessions, and virtually no difference between sessions. This,
in turn, is the direct result of their fear (of the prey) having been
attenuated beforehand through the experience of pre-exposure. On the
other hand, the exploration rate for the subjects in the Perforated
group dropped significantly on the second test session. The relatively
high rate on session one could be explained in terms of the added
opportunity for tactile exploration with the vibrissae (an experience
they did not receive during pre-exposure). Consequently, the experi-
ence gained via the tactile modality on session one resulted in a

decrease in the frequency of exploration on session two.

10.2.   EXPERIMENT 6b: THE INFLUENCE OF AGE AND TREATMENT -

TEST INTERVAL.

Having now substantiated the beneficial effects of pre-exposure

it seemed worthwhile to determine if the effect was limited to a

certain time in ontogeny or if the interval which intervened between

exposure and test was of any importance.   Therefore the experiment

reported below set out to ascertain what influence, if any, these

two factors had.   Hence, it was similar in purpose and design to

Experiment 5b (Chapter 9).

10.2a.   Design and Procedure

The subjects were 47 hamsters derived from five litters born

between 22nd December, 1973 and 4th January, 1974.   All were weaned

at 23 or 24 days of age, weighed, sexed and placed individually in

a testing compartment.   Subjects within each litter were assigned

to the following groups on the basis of their matched weights:

Group 1 : Early Exposure - Early Test   (EE - ET)

Group 2 : No Exposure - Early Test (NE - ET)

Group 3 : Early Exposure - Early Test (EE - ET)

Group 4 : Late Exposure - Late Test (LE - LT)

Group 5 : No Exposure - Late Test (NE - LT)

Subjects in the two early exposure groups were initially pre-exposed to the prey commencing on Day 26 (either 2 or 3 days subsequent to weaning). Exposure for the late test group (e.g. group EE - LT) continued until Day 31 (i.e. Days 26 - 30 inclusive) and for the early test group (e.g. group EE - ET) exposure continued until the completion of testing. Subjects in the late exposure group (LE - LT) were pre-exposed to the prey starting on Day 46 and exposure continued until the completion of testing. Subjects in the No Exposure - Early Test (NE - ET) and No Exposure - Late Test (NE - LT) groups had an empty perforated cube placed into their compartment starting on Day 26 or 46 respectively, and it remained in the compartment until the completion of testing.

Testing commenced for all subjects either early (31 days of age) or late (51 days of age). Thus, for example, out of the two groups which were pre-exposed early, one was tested early and the other tested late. Therefore, for the EE - ET group the interval which intervened between treatment and test was nil. On the other hand, the interval which intervened between treatment and test for the EE - LT group was 21 days.

In summary, subjects in the EE - ET group were pre-exposed starting at 26 days of age. Exposure continued for this group throughout testing, which commenced on Day 31. Subjects in the NE - ET group were pre-exposed only to an empty cube prior to testing (which likewise commenced on Day 31) and throughout testing. EE - LT subjects were pre-exposed to the prey between Day 26 and Day 31; on Day 31 the cube was removed and testing commenced 21

days later (Day 51). For LE - LT subjects pre-exposure commenced

on Day 46 and it continued throughout testing, which commenced on

Day 51. Subjects in the last group, NE - LT, were treated in a

manner identical to that of LE - LT subjects except that the cube

to which they were exposed contained no prey.

Testing consisted of introducing an active 4th instar locust

into a subject's compartment. Tests continued once daily until a

subject captured, or until three successive tests without capture.

At most, then, subjects were tested, in total, on three occasions.

On all tests a maximum of five minutes was allowed for capture;

if no capture occurred within this time the prey was removed and

the session terminated. The principal measure taken during testing

was latency to capture, and this was recorded on a stop watch. During

the entire course of the experiment subjects had ad lib access to

food and water.

10.2b. Results

Loss of Subjects. One subject in the EE - LT group (M4) died

before the completion of testing; hence data was collected from

only seven subjects in this group. In the EE - ET, and NE - ET

groups all subjects assigned (4 males and 5 females each) completed

testing; hence data were collected from nine subjects in each

group. In the LE - LT group one subject escaped from its compartment

(F3) on the day of test commencement; this subject was discarded
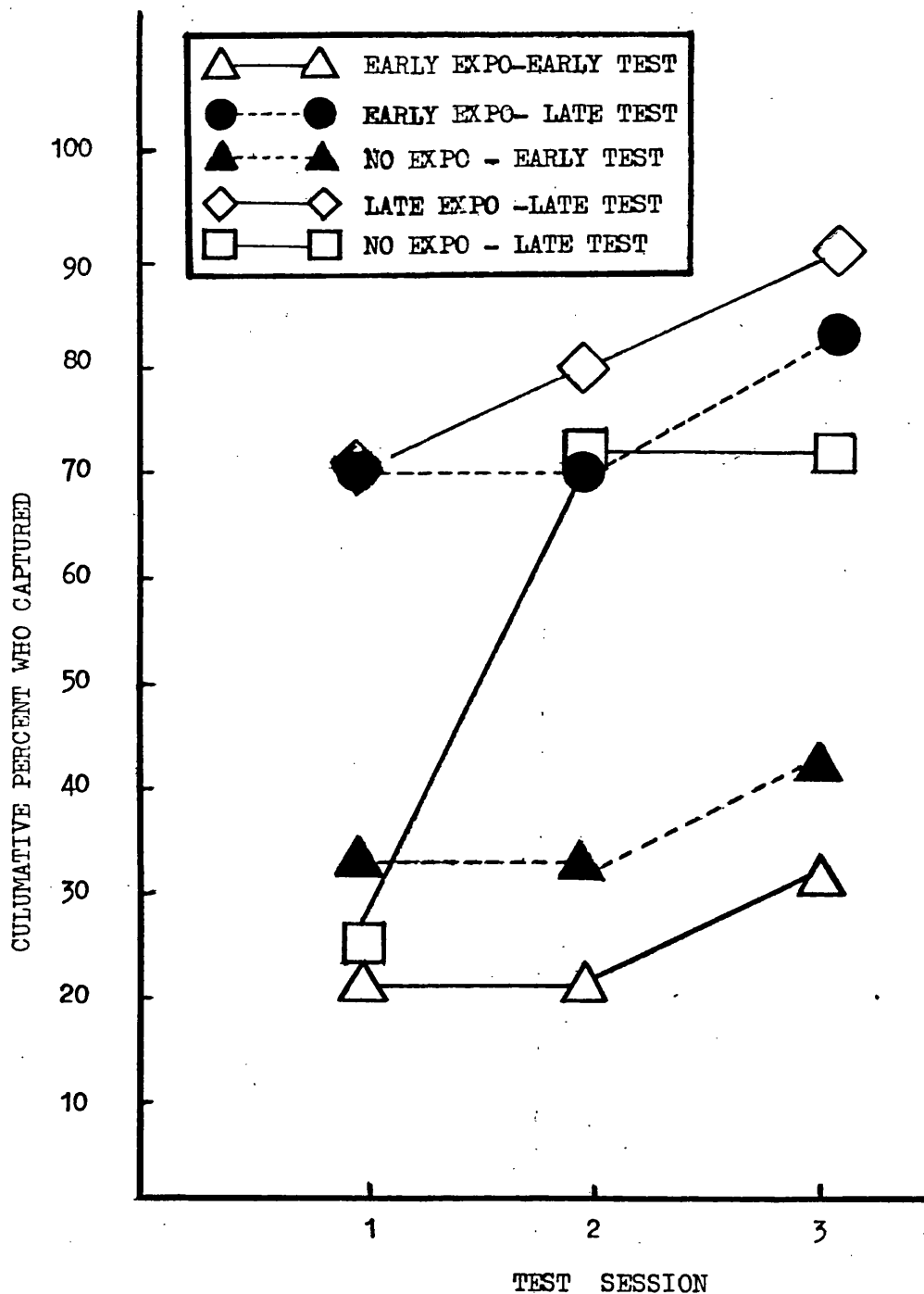
Figure 10.4. Cumulative percent within each age
group of Experiment 6b which made at least one capture.
Subjects were tested once daily until they made a
successful capture, or until they fulfilled the
criterion of no capture on three successive tests.
Males and females within each group have been
combined. See text for further details.

from the experiment. Data were therefore collected from 10 subjects

in the LE - LT group. In the NE - LT group, one subject (F2) escaped

from its compartment during the treatment phase; it was subsequently

captured and placed back into its compartment on the day before the

initial test. This subject was then tested once and it failed to

capture (latency score of 300 seconds). A second test was not given

because of the Experimenter's decision to discard the animal from

the experiment (due to it having escaped); hence this subject's

score was not included in the statistical analysis. Another subject

in the NE - LT group (F3) was tested and captured with a latency

of 31 seconds; however, at the time of testing the Experimenter

noticed that this subject's compartment contained no food. It was

difficult to determine how long subject F3 had been deprived of food

(probably about one or two days), but knowing the strong effect food

deprivation has on the initiation of capture in the naive subject

(substantiated by this author in several experiments).it seemed

prudent to discard it from the experiment. Hence, in total, data

were collected from eight subjects in the NE - LT group.

Raw data in terms of latency to capture for the 43 subjects which

completed testing appear in Appendix B, Table 31.

Cumulative Percent of Captors (see Figure 10.4). The latency

data has been treated in the first instance in a nominal fashion

(i.e. having captured or not having captured) with a Chi-square

test for independent samples. The number of captors on any partic-

ular test session were based on the cumulative total of subjects which
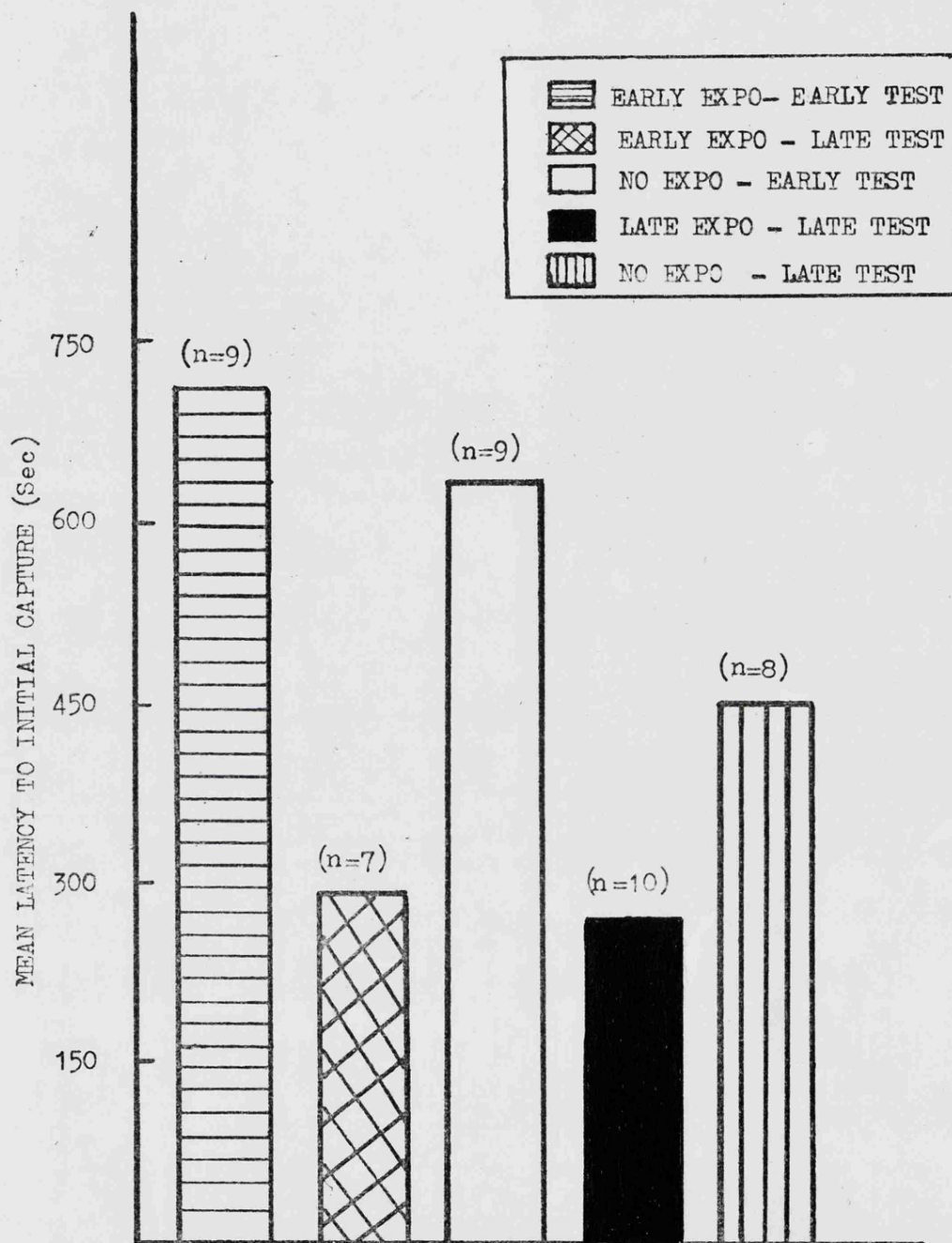
Figure 10.5. Mean latency to the initial capture
for the five groups in Experiment 6b. Subjects
were tested once daily until they captured, or
until they met the criterion of no capture on three
successive tests. Subjects were tested, at most,
on three occassions. The maximum latency score that
could have been achieved was therefore 900 sec.
Latency scores for the males and females within each
group have been combined. See text for further details.

captured prior to and on that test session. Thus, for example,

only two subjects out of eight captured on test session one in the

NE - LT group, as Figure 10.4 indicates. However, after the second

session, 4 additional subjects from this group captured, thus making

a cumulative total of six (75%). On the last session the two subjects

in the NE - LT group which failed to capture on the first two sessions

again did not capture; hence the cumulative total remained at 75%

(6 out of 8). Using these cumulative totals, one-tail Chi-square

tests revealed that the five groups differed significantly from each

other on all three test sessions (session one, $X^2 = 7.95$, df = 4,

$p < .05$; session two, $X^2 = 10.19$, df = 4, $p < .025$; session 3,

$X^2 = 10.05$, df = 4, $p < .025$). In terms of the actual percent

which captured Figure 10.4 shows, for example, that 22% of the

EE - ET group captured (on session one) as opposed to 71% of the

EE - LT group. On session two, the cumulative number of captors

increased in three of the five groups, and on the last session there

was again a slight increase for most groups.

Cumulative Latency to Capture (see Figure 10.5). Latency data

was treated in the same manner as above; that is, by taking the

cumulative time to the initial capture. Thus, to take an example,

Subject F4 of the EE - ET group failed to capture on the first two

test sessions, but captured on the third with a latency of 180

seconds (see raw data). The cumulative latency to the initial

capture for this subject was therefore 780 seconds. The mean cumul-

ative totals for each group are presented in Figure 10.5. A Kruskal-

Wallis one way analysis of variance showed that differences among the

five groups were significant (H = 8.59, df = 4, p <.05). Individual

comparisons between groups were made with the Mann-Whitney U test.

Significance emerged between the EE - ET and the LE - LT groups

(U = 23, p <.05, one-tail) and differences between the EE - ET

and EE - LT group also reached significance at the .05 level with

a one-tail test (U=15, p = .05). Differences between the NE - ET

and the NE - LT and between the NE - LT and LE - LT fell short of

significance with two-tail tests (U = 25, p > .10 for the NE - ET

vs. NE - LT comparison; U = 26.5, p > .10 for the NE - LT vs.

LE - LT comparison).

10.2c. Discussion

The results of this experiment are consistent with the

results of Experiment 6a. Generally speaking, they again demon-

strate that the incidence of capture in the naive hamster can be

significantly increased through sensory pre-exposure to the prey.

Moreover, the results are interesting in that they show that pre-

exposing hamsters early in ontogeny (immediately after weaning),

coupled with early testing has relatively little affect when compared

with subjects which were pre-exposed early and tested late, or pre-

exposed late and tested late. This, then, suggests that it is the

age of a hamster at the time of the test and not the age at exposure

or the interval between exposure and test which determines the magni-

tude of the pre-exposure effect.

The importance of age in determining what effect pre-exposure

might have can be more fully appreciated if one reconsiders the
following group comparisons:

1) EE - ET vs. EE - LT: Here the difference was large,
significant and in the expected direction. Hamsters in both groups
were pre-exposed early, but subsequently one group was tested early
and the other late. This difference must therefore be attributed to
the age at testing.

2) NE - ET vs. NE - LT: The mean cumulative latency to the
initial capture for each group was 629 and 449 seconds, respectively.
This difference, however, fell short of statistical significance
(perhaps in part due to the small sample size). It should be noted,
though, that the difference was in fact fairly large, in the expected
direction and further, consistent with the findings of Experiment 1
(Chapter 5).

3) EE - LT vs. LE - LT: The mean cumulative latency for each
group was 296 and 270 seconds, respectively. If the interval between
treatment and test was important, then one would have expected the
difference between these groups to be much larger. Therefore it
seems that exposure at either age is effective as long as it is
paired with a late test.

4) EE - ET vs. NE - ET: Here the difference was small and
in the direction opposite to what would have been expected. This
result, as stated above, suggests that in order for early pre-exposure

to have a beneficial effect it must be coupled with a late test.

5) <u>NE - LT vs. LE - LT</u>: The difference between these groups was in the expected direction and relatively speaking much larger than the difference between the EE - ET vs. NE - ET groups. This result thus suggests that the effects of pre-exposure are genuine and open to demonstration, but only if pre-exposure is coupled with a test relatively late in ontogeny.

The last comparison mentioned is particularly interesting because the difference between the two groups did not reach significance but only approached it (p $<$ .20). This lack of significance could stem from the fact that when a hamster reaches a certain age the chances of capture become just as likely whether it had been previously pre-exposed to the prey or not. This reasoning is conceivable in light of what is known about the maturational aspects of the response (i.e. the chances of capture in the naive subject increase in a linear fashion with age; see Experiment 1, Chapter 5). If this is true, then it suggests an inverted U - shape function for whatever effects pre-exposure might have (or for that matter any other treatment administered to a naive hamster prior to its first test for prey capture). That is, to be specific, hamsters pre-exposed early (say around 25 days of age) and tested early (say around 30 days) should capture with latencies comparable with that of controls (i.e. those which were not pre-exposed). Moreover, hamsters pre-exposed early (or perhaps late - as we now know, this variable is relatively unimportant) and tested late (say between 40 and 50 days) should show a

relatively high incidence of capture when compared with controls,

due to the effects of pre-exposure. Lastly, if hamsters were

exposed late, or even early, and then tested at a relatively late

age (say around 90 days) then they should, hypothetically, show no

difference in the incidence of capture when compared with controls

tested at the same age. The reason for this is, with a relatively

late test, the variable of age would override the positive effects

of pre-exposure.

10.3. GENERAL DISCUSSION

The independent variable under scrutiny in the two experiments

reported in this chapter, namely that of sensory pre-exposure, is

very similar in kind to the variable investigated by E. Noirot in

her studies on maternal behaviour in domestic mice. From a long

series of experiments (see Noirot, 1972 for a review) she has

gathered evidence indicating that the maternal responsiveness of

naive mice (of both sexes) can be significantly increased through

a period of pre-exposure to the relevant stimulus object.

For example, in one experiment (Noirot, 1969) naive mice

were pre-exposed only to the auditory and olfactory stimuli emanating

from a day old pup (a strong releaser for maternal behaviour) hidden

in a small perforated tin. Tactile and manipulatory experience with

the pup were impossible. When subsequently tested with a drowned

pup (supposedly a weak releaser for maternal behaviour) experimental

subjects were more likely to exhibit maternal behaviour such as

retrieving, crouching, licking and nest building than non-pre-exposed

controls. Noirot used the word 'priming' to describe this phenomenon,

(in the sense that the maternal responses were primed into condition

as a result of pre-exposure) and emphasized that it differed from

straightforward 'learning' in that the increased readiness to show

maternal behaviour with the drowned pup occurred in the absence of

prior performance (i.e. no prior opportunity to practice maternal

behaviour during pre-exposure) and in the absence of the cues needed

to elicit the behaviour (i.e. cues from the drowned pup supposedly

differed from those of the newborn pup).

Now it does not take much to realize that the effect she

obtained was very similar in kind to the effect obtained in the two

experiments reported in this chapter, albeit with a different species

and with a different behaviour in question. Assuming, then, that a

hamster's predatory tendencies can be primed much in the same way

as maternal responsiveness in mice, then one wonders if other types

of hamster behaviour are susceptible to the same effects.

The one single experiment relevant to this point, that of Noirot

and Richards (1966), which demonstrated that a naive hamster's mater-

nal responsiveness could be primed, was discussed in Chapter 3. Again,

though, very briefly, the procedure in their experiment consisted of

proffering a naive hamster a hamster pup of the age of one, five or

nine days for a period of 15 minutes. Tests were then conducted two

days later with a five day old pup. The results were clear in that

they suggested that priming did take place, for hamsters were consid-

erably more maternal during the test than during the initial 15
minute exposure. Concerning this point, Noirot asserts, "the
fact that maternal behaviour has been increased after the animals'
initial contact with 1 day old pups shows that, as in rats and mice,
the change is independent of the performance of maternal responses.
Indeed, in this group all the females had attacked, killed and
eaten only one day old pups, and none had displayed any sort of
maternal care. Therefore again the increase seems to result from
the animals' mere exposure to the cues from the pups, and resembles
the process described as sensitization in the rat, and as priming
in the mouse" (pp. 121 - 122).

It therefore seems that the experience with the appropriate
stimulus object, whether it be prey or a pup, plays a similar role
in both the development of hamster maternal behaviour and a hamster
predatory behaviour. To further clarify this point, take Noirot
again, who in her writings has emphasized that inexperienced subjects,
whether they be males or non-parturient females, "need a certain time
during which they are caged with the pups before they overcome their
initial tendency to avoid, explore, or attack, and become fully
maternal. The amount of time varies greatly with the species and
environmental circumstances: it may be as short as 1 or 2 minutes
or as long as 2 weeks" (p-108). As we know, like the naive rat or
mouse confronted for the first time with a novel pup, the naive
hamster too needs a certain time during which it is caged with the
novel prey before it will attempt capture (Experiment 1, Chapter 5).
Further, we know that this amount of time varies greatly between

individuals, and we also know that during the initial phases of

the confrontation the behaviour is fundamentally the same as it

is with the rat confronted with a pup, or mouse.[1] That is,

ambivalence characterized by approach - withdrawal. The process

which brings about the waning of ambivalence and the subsequent

increase in the likelihood of maternal responsiveness Noirot, as

previously mentioned, has called priming. The only apparent dif-

ference between this process and the process this author has

postulated to account for the gradual development of naive hamster's

predatory tendencies is one of terminology. In the previous

chapters it has been repeatedly stressed that it is the experience

of exposure, or the process of habituation, which brings about the

waning of ambivalence (towards novel prey) and eventually capture.

It therefore appears that the process governing the ontogeny of

hamster maternal behaviour has features in common with the process

controlling the onset of hamster predatory behaviour.

1. Hamsters, on the other hand, differ from rats and mice in that
   when one first tries to prime their maternal response with say
   a one or five day old hamster pup, they will usually attack
   rather than behave ambivalently, maternally or with indifference.
   This has already been mentioned in the text. Eventually, as
   Noirot and Richards (1966) have demonstrated, the maternal
   response in nearly all hamsters will come forth when sufficiently
   primed. Hence, like prey-capture, it seems that all have the
   potential to exhibit this behaviour.

11

THE GENETIC INFLUENCE : SELECTIVE BREEDING EXPERIMENTS

In this chapter, the last in Section II, data gathered from
this author's programme of selective breeding will be presented.
The rationale behind the programme was simple and in purpose it
was similar to the breeding programmes reported by Broadhurst (1960)
for emotional reactivity, Lagerspetz (1964) for inter-male aggression,
Rundquist (1933) for motor activity and Tryon (1942) for maze learn-
ing. Basically, it consisted of breeding male locust captors with
female captors and likewise male non-captors with female non-captors
with the intent of producing two distinct strains of hamster (a
strain of Captors and a strain of Non-Captors).

11.1. METHOD

The breeding programme was initiated in March, 1972, and it
continued uninterrupted for approximately 24 consecutive months
until its cessation in March, 1974. In total, the programme prog-
ressed through eight generations in each of the selected directions;
that is, data from eight generations of the Captor strain were
obtained, along with comparable data from eight generations of the
Non-Captor strain.

Controlled breeding in the proposed directions was initiated

by selecting from the hamster population this author maintained

approximately a dozen proven male and female captors. Likewise,

proven non-captors of each sex were also selected. These animals

constituted Generation 0. All were then subsequently mated (male

captors with female captors and male non-captors with female non-

captors) according to the methods outlined in Chapter 4 (in most

cases the pen breeding method was employed). Females, when pregnant,

were transferred to their own individual maternity cage (specifica-

tions of which were described in Chapter 4) where they subsequently

gave birth and raised their litter. The procedures during gestation

and lactation, food given to the mothers and pups, etc. were identical

in all respects to those employed in the experiments reported in the

previous chapters; for details of the general procedures the reader

should refer to Chapter 4.

Females, constituting Generations 0 through 7, their pups

(i.e. subjects constituting Generations 1 through 8) and the raw

latencies to capture are listed in Appendix B, Table 33 for the

strain of Captors and Table 32 for the strain of Non-Captors.

The reader for the moment should ignore the latency data in

each of these tables and note, for example, that subjects in the

strain C1 (e.g. Captor strain, Generation 1) were derived from five

females and subjects in the strain NC1 (e.g. Non-Captor strain,

Generation 1) were derived from six females. The females chosen to

form Generation 0 were the subjects which became pregnant first out

of the dozen selected; hence in order to expedite matters they were

chosen to bear the pups of Generation 1. The other females and

their litters were discarded.

The first generation of pups were weaned, weighed and sexed

between 23 and 25 days of age. All were then housed individually

in a testing compartment and left undisturbed until the commence-

ment of testing. Tests for locust capture were administered init-

ially at 38, 39, 40 or 41 days of age and continued once daily until

a subject captured successfully, or until the criterion of three

successive tests without capture was met. At most, then, subjects

were tested on three occasions. Active 4th instar locusts were

employed on all tests and subjects were allowed a maximum of ten

minutes (600 seconds) on each test to capture.[1] Latencies to

capture were recorded on a stop watch.

The procedures outlined above were followed for all subsequent

generations (i.e. Generations 2 through 8). Further, upon the com-

letion of testing for any given generation, the fastest male and

fastest female captors of the Captor strain (between 6 and 12 of

each sex) were selected and housed communally so that pregnancy

could be induced in the females. Likewise, non-captors of both

[1] The maximum length of a test session in the breeding programme
     was increased to ten minutes (rather than five minutes as in
     previous experiments). This step was taken in order to ensure
     that adequate time was given on any one test for the develop-
     ment of the capture response. Without enough time the response
     of capture might not have developed in the strain of Captors;
     if this occurred then the differences between the two strains
     would have been small.

.sexes (between 6 and 12 of each sex) in the Non-Captor strain,

or subjects which captured with the highest latencies, were selec-

ted and treated in a similar manner. Whenever possible, the males

and females selected from each strain were housed communally with

their litter mates in order to produce litters arising from brother -

sister matings. That is to say, female non-captors of a litter were

exclusively bred with male non-captors of the same litter. Due to

the variability of the results for the first generation in each

strain, matings of this type were difficult to obtain; however,

for Generations two through eight the subjects were exclusively

the result of brother - sister matings.

In summary, the procedures described above continued in a

cyclic manner over a two year period. At the end of this time,

when the breeding programme was regretfully terminated, this author

had progressed through eight generations in each strain. Again,

very generally, the programme consisted of systematically selecting

and breeding the captors and non-captors from the Captor and Non-

Captor strains, respectively. Their offspring (the next generation)

were then tested at approximately 40 days of age for the capture of

locusts. Upon the completion of testing, selection among the subjects

again took place. Those selected constituted the parents for the

next generation.

11.2. RESULTS .

The score assigned to all subjects was latency to capture.

Table 11.1. Means, variances, and standard deviations for
the latency data of the Captor strain and Non-Captor strain,
generations one through eight. The sample size for each
generation is listed under N. Subjects within each strain
were initially tested at 40 days of age. Tests lasted a maximum
of 10 minutes and continued once daily until a subject made a
capture, or until the criterion of three successive tests
without a capture was met. Therefore the maximum latency a
subject could have achieved was 1800 sec. Latency scores for
the males and females have been combined. All raw scores have
been divided by 100. See text for further details.

| GENERATION | STRAIN | | | | | | | |
| | CAPTOR | | | | NON-CAPTOR | | | |
	N	M	SD	VAR	N	M	SD	VAR
1	37	9.02	7.25	52.47	42	5.58	6.69	44.73
2	37	3.88	5.75	33.13	31	13.92	6.96	48.50
3	28	4.84	6.56	43.03	28	12.44	7.09	50.11
4	26	6.67	7.63	58.32	36	9.78	8.11	65.82
5	36	3.37	4.97	24.74	34	9.40	8.16	66.63
6	38	2.75	5.09	25.94	44	15.97	4.43	19.62
7	34	5.83	6.88	47.33	35	13.30	7.58	57.47
8	44	2.83	4.86	23.62	27	15.33	5.55	30.80

Table 11.2. T values based on the difference in latency to
capture for the strain of Captors versus the strain of
Non-Captors. T values for generation one through eight are
presented. The mean latency to capture for each strain on
each generation is presented in the brackets. The values
listed in the right hand column indicate the probability
level associated with the t score for any given comparison.
All probabilities are based on two-tailed tests. Latency scores
for the males and females within each strain have been combined.

GENERATION	T VALUE CAPTOR	NON-CAPTOR	df.	PROB.
1	(902) 2.20	(551)	77	<.05
2	(386) 2.67	(1392)	66	<.01
3	(484) 3.37	(1244)	54	<.01
4	(667) 1.61	(975)	60	<.20
5	(337) 3.76	(940)	68	<.01
6	(275) 10.49	(1598)	80	<.005
7	(583) 4.29	(1301)	67	<.01
8	(296) 10.00	(1532)	69	<.005
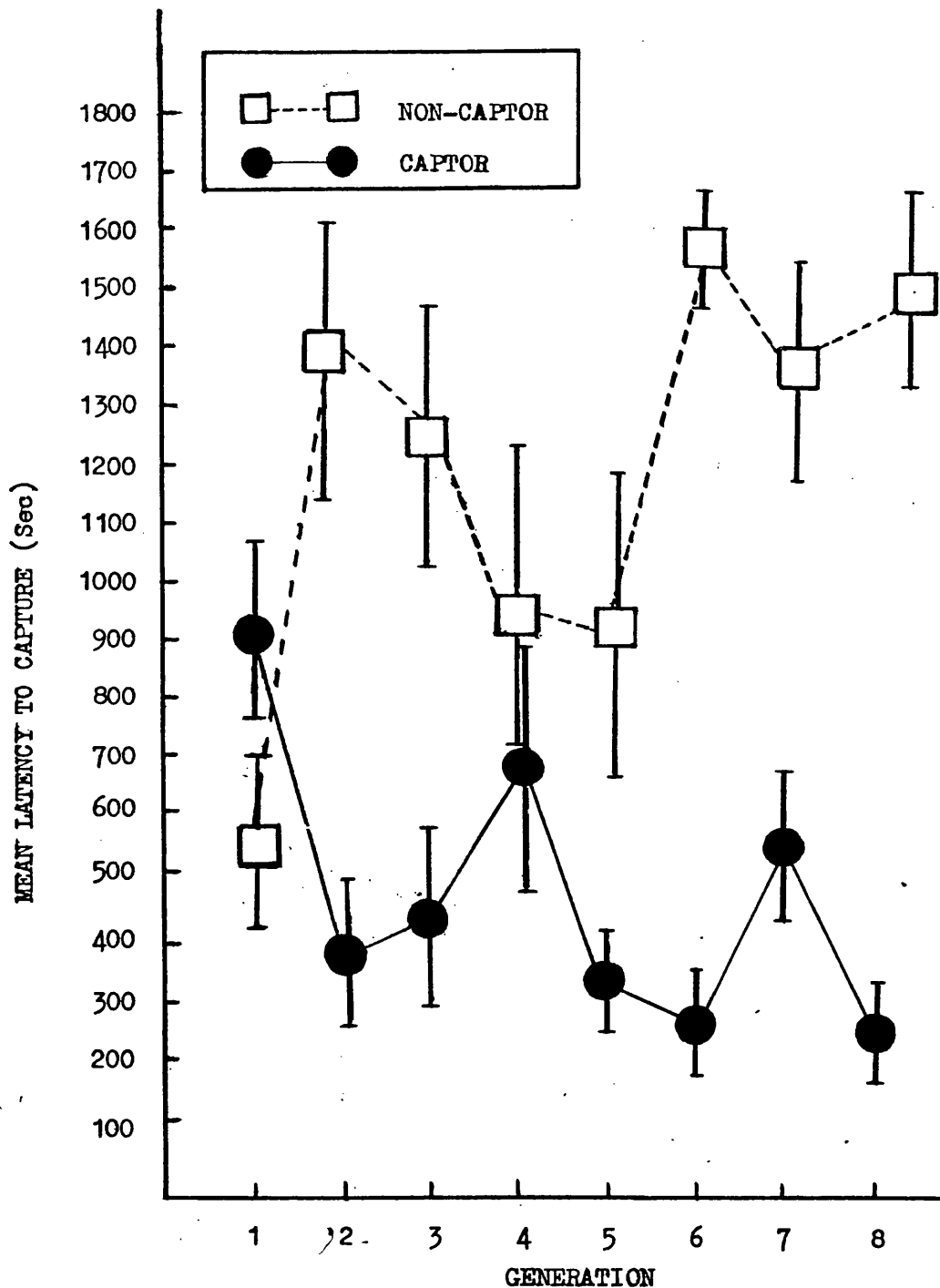
Figure 11.1. Mean latency to capture for each strain over eight generations of selective breeding. Vertical bars indicate the standard error. Latency scores for the males and females have been combined. See text for further details.
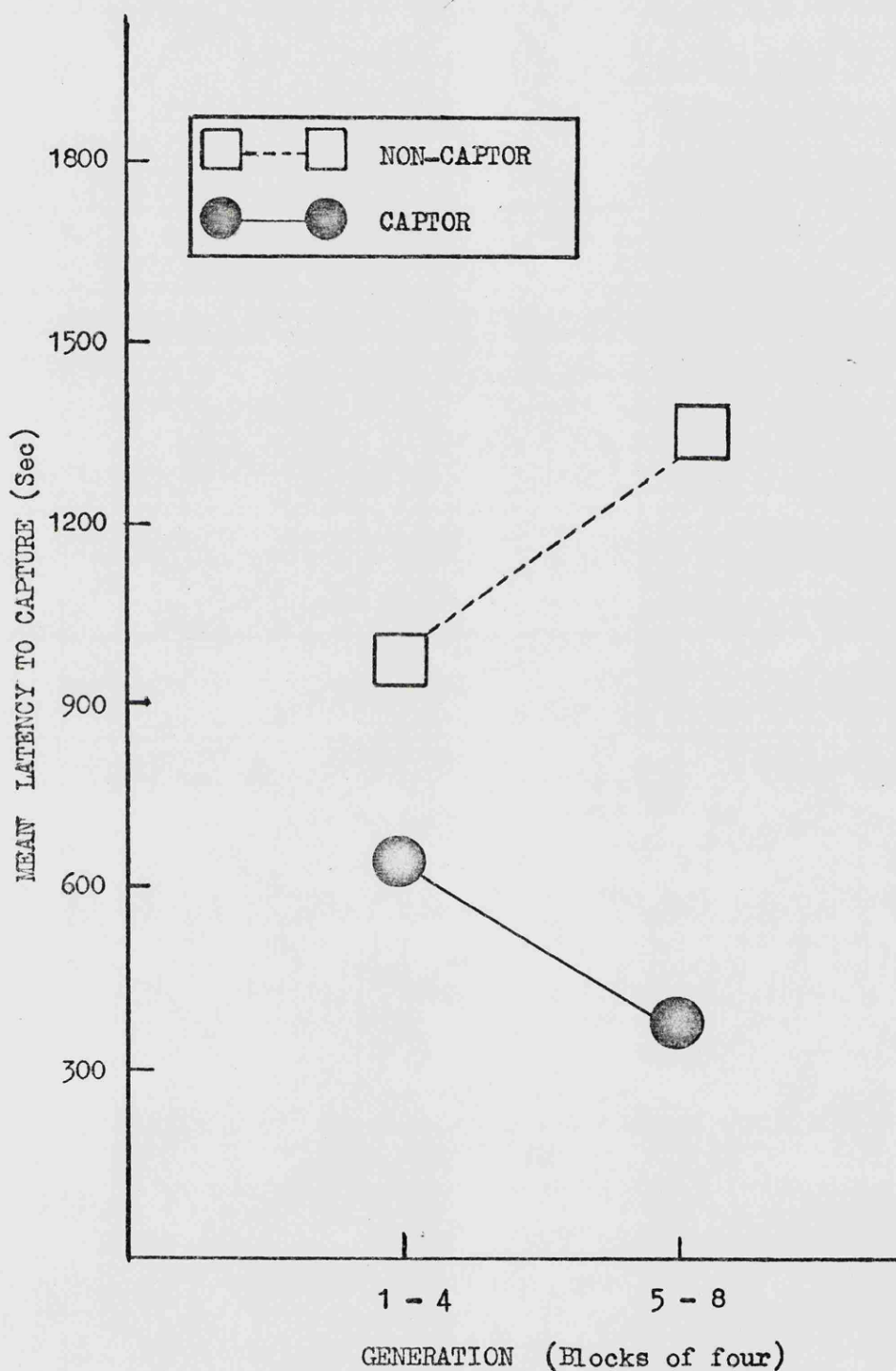
Figure 11.2. Mean latency to capture for the strain
of Captors and strain of Non-Captors over eight generations   of
selective breeding. Latency data for the eight
generations has been combined into two successive
blocks of four each. Males and females within each
generation have been combined. See text for additional
explanation.

Subjects which failed to capture on all three tests were accordingly

assigned the score of 1800 seconds.

The data has been summarized in the following tables and graphs

in the text:

Table 11.1. Here the sample size for each generation is pres-
ented along with the mean latency to capture (raw scores have been

divided by 100), the standard deviation and variance.

Table 11.2. This table lists t values based on the difference

in latency to capture for the strain of Captors versus Non-Captors on

each generation. Probability levels associated with these values are

also given.

Figure 11.1. In this figure mean latencies to capture for all

generations are graphically presented. The standard errors are

also indicated.

Figure 11.2. In this figure latency scores for each strain have

been blocked into successive groups of four each and the means graph-

ically presented. Latency scores for the males and females within

each strain have been combined.

A summary of the results for each strain in each generation will

now be presented. The reader should refer to the tables and graphs

listed above when the need arises.

Strain of Non-Captors

Generation NC1: Forty-five subjects (born between 12th July and 15th August 1972) were derived from six litters. Out of the 45, forty-two subjects completed testing (20 male and 22 female). The three subjects which failed to complete testing (M4, M11,F2) died before test commencement. Inspection of Table 11.1 shows that the mean latency to capture for this generation, males and females combined, was 558 seconds. Of the 42 subjects tested, six failed to capture for a non-capture incidence of 14%. The subjects selected for breeding for the next generation were the following: M3, M8, M14, M22, F8, F9, F12, F20, F22, F23.

Generation NC2: Thirty-two subjects were derived from five litters. All were born between 7th October and 27th October 1972. Out of the thirty-two, 31 subjects completed testing (14 male and 17 female). The subject which failed to complete testing, due to having died prior to test commencement, was F2. Inspection of Table 11.1 shows that the latency to capture for this generation was 1392 seconds. Twenty subjects failed to capture for a non-capture incidence of 65%. The subjects selected for breeding were the following: M2, M3, M6, M8, M9, M10, M11, M14, F4, F5, F6, F7, F9, F11, F14, F15, F16, F17, F18.

Generation NC3: The sample size for this generation was twenty-eight. All were born between 8th January and 15th January 1973. Out of the 28, fifteen were male and thirteen female. Table 11.1 shows

that the mean latency to capture for this generation was 1244 seconds. Fifteen subjects failed to capture for a non-capture incidence of 54%. The subjects selected for breeding were the following: M1, M3, M7, M9, M11, M13, F1, F2, F3, F4, F6, F7, F11, F12.

Generation NC4: The sample size for this generation was 36 (18 male and 18 female). Subjects were born between 25th March and 30th March 1973. The mean latency to capture for this generation was 978 seconds. The incidence of non-capture was 44% (sixteen failed to capture). The subjects selected for breeding were the following: M4, M7, M8, M10, M13, M14, M17, M18, F5, F7, F9, F12, F13, F14.

Generation NC5: Thirty-six subjects were derived from six litters. All were born between 8th June and 23rd June 1973. Out of the 36, two died (M13, M14) before test completion, thus leaving a sample size of 34, of which 17 were male and 17 female. Mean latency to capture for this generation was 940 seconds (see Table 11.1) and the non-capture incidence was 44% (15 out of 34). The subjects selected for breeding for the next generation were the following: M1, M3, M4, M6, M12, M16, M18, F3, F4, F5, F6, F10, F16, F17.

Generation NC6: Subjects were derived from six litters and all were born between 25th August and 28th August 1973. One male (M4) died before the completion of testing; hence this left 26 males and 19 females (sample size of 44). The incidence of non-capture

for this generation was 80% (35 out of 44) and the mean latency to

capture was 1597 seconds (see Table 11.1). The subjects selected

for breeding were the following: M1, M3, M4, M6, M12, M16, M18,

F3, F4, F5, F6, F10, F16, F17.

Generation NC7: The selection procedures for this generation

differed slightly in that approximately half the pups from each

litter were randomly selected and assigned to a different experi-

ment (not reported in this treatise). The remaining subjects (16

male and 19 female) were treated in the usual fashion; that is,

weaned, weighed, sexed, placed in an individual testing compartment

and then tested for locust capture starting at approximately 40 days

of age. Subjects were born between 3rd November and 16th November

1973. The incidence of non-capture was 71% (25 out of 35) and the

mean latency to capture was 1330 seconds. The subjects selected

for breeding were the following: M3, M5, M6, M7, M8, M10, M11, M12,

M14, M15, F5, F6, F7, F8, F10, F11, F12, F13, F17. In addition,

littermates which were assigned to the other experiment were also

used for breeding purposes.

Generation NC8: Thirty-two subjects were derived from six

litters. All were born between 20th January and 8th February 1974.

Five subjects (M7, M8, M10, M13, F14) died before test commencement,

thus leaving a sample size of 27 (12 males and 15 females). The mean

latency to capture for this generation was 1553 seconds (see Table

11.1) and the incidence of non-capture was 78% (21 out of 27).

The reader should note that subsequent to testing and prior

to breeding, subjects in generations NC4 and NC8 underwent a series

of tests (ambulation in an open field; exploration of a novel

object; T-maze exploration; in addition, subjects in generation

NC4 were tested for capture of a cockroach) in order to determine

if the tendency to capture locusts varied in any way with their

behaviour in these situations. The results gathered from these

tests will not be reported, but they should appear in some journal

in the near future (assuming they get accepted for publication).

Strain of Captors:

Generation C1: Originally the sample size for this generation

was 38. However, one subject (M15) died prior to testing, leaving a

sample size of 37 (18 male and 19 female). Subjects were born

between 9th April and 19th April 1972, and all were derived from

5 litters which ranged in size from five to eleven (see Table 33,

Appendix B). The non-capture incidence for this generation was

32% (12 out of 37) and the mean latency to capture was 902 seconds

(see Table 11.1). The subjects selected for breeding were the

following: M1, M9, M10, M13, M17, F1, F5, F8, F10, F16.

Generation C2: Two subjects (M13, M14) out of the original

39 died prior to test commencement, thus leaving a sample size of

37 (17 male and 20 female) for this generation. Subjects were born

between 28th June and 12th July 1972. The mean latency to capture

was 388 seconds (see Table 11.1) and the non-capture incidence was

10% (4 out of 37). The subjects selected for breeding were the

following: M2, M3, M4, M11, M12, M15, M16, F2, F3, F10, F13, F15,

F16, F17.

Generation C3: The sample size for this generation was 28,

of which 10 were male and 18 female. Subjects were derived from

five litters born between 9th September and 18th September 1972.

The incidence of non-capture for this generation was 14% (4 out of

28) and the mean latency to capture was 484 seconds (see Table

11.1). The subjects selected for breeding were the following:

M2, M3, M7, M8, M10, F3, F4, F5, F9, F10, F13, F15.

Generation C4: The sample size for this generation was 26.

Subjects were born between 1st December 1972 and 14th January 1973.

The five litters from which the subjects were derived ranged in

size from two to six. Out of the twenty-six, 14 were male and 12

female. The mean latency to capture for this generation was 667

seconds (see Table 11.1) and the non-capture incidence was 23%

(6 out of 26). The subjects selected for breeding were the following:

M4, M6, M10, M12, M13, M14, F1, F6, F7, F8, F10, F11.

Generation C5: The sample size for this generation was 36.

Subjects were born between 6th April and 12th April 1973. All

were derived from six litters, which ranged in size from five to

seven (see Table 33, Appendix B). Out of the thirty-six, 19 were

male and 17 female. The mean latency to capture was 337 seconds

(see Table 11.1) and the non-capture incidence was 5% (2 out of 36).

The subjects selected for breeding were the following: M5, M6,

M8, M9, M11, M12, M16, M17, F5, F7, F8, F10, F11, F12, F16, F17.

Generation C6:   A sample size of 38 (18 male and 20 female),

born between 23rd July and 29th July 1973, was derived from six

litters. All litters contained six or seven pups (see Table 33,

Appendix B). Further, all of the pups in two of the litters

(those of ♀♀4 and ♀♀6) were albino. The mean latency to capture

for this generation, 275 seconds, was the lowest value achieved

for the strain of captors (see Figure 11.1). The incidence of non-

capture was also very low, 5% (2 out of 38). The subjects selected

for breeding were the following: M1, M2, M3, M10, M11, M15, M16,

M18, F1, F2, F3, F12, F18, F19, F20.

Generation C7:   Three of the six females selected to bear the

subjects for this generation produced offsprings that were all albino

(♀♀1 ♀♀2 ♀♀4;   see Table 33, Appendix B). In total, 37 subjects were

derived from the six females. Subjects were born between 6th October

and 3rd November 1973. Subsequently three died (M14, M18, F4) before

the onset of testing, thus leaving a sample size of 34 (18 male and

16 female). The mean latency to capture for this generation was

583 seconds (see Table 11.1) and the incidence of non-capture was

17% (6 out of 34). The subjects selected for breeding were the

following: M7, M13, M15, M16, M17, M19, F5, F6, F7, F9, F10, F11,

F12, F15, F16.

Generation C8:   All of the pups from four of the seven females

selected to bear the subjects for this generation were albino

(♀♀1 ♀♀2 ♀♀3 ♀♀4). In total, from the seven litters, born between

12th December 1973 and 16th January 1974, forty-four subjects were

derived (litters ranging in size from four to eight) of which 23

were male and 21 female. The non-capture incidence for this gener-

ation was 6% (3 out of 44) and the mean latency to capture was 283

seconds (see Table 11.1).

The reader should note that like the subjects in the Non-Captor

strain, subjects in the Captor strain, generations four and eight,

were also administered a battery of tests (identical to that admin-

istered to Non-Captors) subsequent to their tests for locust capture

and prior to breeding (prior to breeding, as it is meant here, is

only applicable to the subjects of generation four; subjects in

generation eight were not bred).

Statistical Analysis

T-values, based on the difference in latency to capture for

the strain of Captors versus the strain of Non-Captors for each

generation are presented in Table 11.2. The data are graphically

presented in Figure 11.1. For generation one, the results show that

the reverse of what was expected occurred; that is, Non-Captors

captured with a significantly shorter latency than the Captors and

this difference, surprisingly, was significant (p < .05). However,

on Generation two, and on all subsequent generations, the difference

reversed itself (i.e. the Captors had lower latencies than the

Non-Captors), and in all cases, except Generation four, the differ-

ence was significant.

Next, the latency data for both strains was blocked into

successive groups of four each (i.e. generations 1 - 4 combined

and generations 5 - 8 combined). The means appear graphically in

Figure 11.2. Two-tail t-tests were applied to this data for bet-

ween strain comparisons on each block and between block comparisons

for each strain. First, in regards to the between-strain comparis-

ons, the Captor strain had significantly shorter latencies than the

Non-Captor strain on both blocks one and two (t = 4.16, df = 263,

p < .01 for block one; t = 13.68, df = 290, p < .001 for block two).

In regards to the between block comparisons, the Captor strain

captured with a significantly shorter latency on block two when

compared with one (t = 3.37, df = 278, p < .005) and the Non-

Captors captured with a significantly higher latency on block two

when compared with block one (t = 4.07, df = 275, p < .005).

11.3. DISCUSSION

The results gathered from the programme of selective breeding

were, on the whole, clear cut and therefore indicative of the strong

effect genotype has on the development of locust capture. Further,

they are important in the sense that they help, in part, account for

the great deal of individual variability in the tendency to capture

among randomly bred naive hamsters with similar past experiences.

Thus, as it was argued in Chapter 5, it appears that such individual

variation may be attributed to genotype, and assuming this, it may

be hypothesized that all hamsters possess the potential to capture

with the potential varying in degree from strain to strain and from

individual to individual within any particular strain.

General as it may be, this could be taken as the cardinal

finding of the treatise. Thus realizing the importance of it for

our understanding of hamster predation, additional questions present

themselves in regard to some of the secondary findings of the breed-

ing programme. First, what was the significance of the concomitant

phenotypical change between coat colour and capture latency for the

subjects in the Captor strain from Generation six onwards? It should

be recalled that the majority of Captors in Generations seven and

eight were albino. One wonders, then, just what the relationship was

between albinism and prey capture. Does the albino gene(s) have a

direct causal effect on the behaviour in question, or does it express

its influence through the modification of some other behavioural

system?[2]

---

2. The interested reader should consult the work of J.L.Fuller,
   a prominent researcher in the field of behavioural genetics.
   In one study (Fuller, 1967) he examined what effect albinism
   had on the behaviour (e.g. learning tasks, tests for emotion-
   ality) of laboratory mice. In general, he reported that the
   albinos appeared more stressed by the test procedures when
   compared with pigmented mice. For a more relevant study, one
   should consult Butler (Butler, 1973) who reported a relationship
   (although not statistically significant) between albinism and
   high latencies to predatory attack (crickets being the prey)
   in domestic mice (Mus musculus).

Second, one may ask just how many - in absolute terms - genes
are in control of the behaviour. More exactly, the question becomes
one of determining if hamster predation is under the control of a
single gene, a few genes, or relatively many genes. Although it
would seemingly be ludicrous to argue that the whole series of
behavioural components involved in predation are under the control
of a single gene, or even a few genes, another researcher (Thomas,
1972) in a recent paper on mouse predation asserted "the rapid
response to selection suggests that a small number of genes could
be involved here" (p-6). In this comment Thomas is referring to
her breeding programme (reported in Chapter 2) in which significant
differences were obtained in latency to attack between the strains
selected for after the second generation. And as we know, the
hamster strains selected for in this author's programme of breeding
also diverged very quickly (see Table 11.1), thus suggesting that
the conclusion Thomas came to for mouse predation might also be
applicable to hamster predation.

Third, one might fairly ask, just what was the trait selected
for in this programme of breeding? The underlying assumption the
reader has no doubt been led to is that it was the tendency to
engage in the behaviour of capture per se, or the lack of such a
tendency. However, an interpretation such as this must be treated
with caution, for the change in capture tendency, in either direction,
may well have been due to the concomitant change in some other process
or mechanism. For example, it is possible that this author unknowingly
selected for sensitivity in some sense modality, perhaps olfaction.

Hamsters, then, it could be argued, from the strain of Captors were more likely to capture than those from the Non-Captor strain, in large part because they were able to detect the prey more readily.

If this is true, then it still does not negate the fact that something certainly was selected and whatever the trait, it still nevertheless could be associated with, or have a causal influence on, the tendency to capture. Thus perhaps, if in fact hamsters were selected for olfactory acuity, then this would imply that the ability to smell was a pre-requisite for capture. To further illustrate this point, possibly the trait selected for was emotionality and not olfactory acuity (possibly too, it could have been both). Therefore breeding in the opposite directions produced hamsters which were emotionally reactive to novel stimuli and those which were not. If this was so then it could be reasoned that non-emotional hamsters (e.g. those of the Captor strain), captured because they had less fear of the novel locust when compared with emotional subjects (e.g. those of the Non-Captor strain) which in turn failed to capture because their fear inhibited the tendency to capture. Such an explanation is plausible and it fits in well with the theory developed in the earlier chapters.[3]

---

3. Empirical support for this contention should come from the correlation tests that subjects in Generations four and eight underwent. This author at present is in no position to make a definitive statement on the results, for they have not been analysed in full. However, rough inspection shows that the Non-Captors of generation eight ambulated less in the open field (under high intensity light) than the Captors of generation eight, thus suggesting that they may have been more emotional.

Finally, one shortcoming of the breeding programme stems from the fact that the latency scores of the Captor and Non-Captor strains were not compared and analysed against data from an unselected strain. This procedurally would have been difficult to accomplish, for space limitations prohibited the maintenance and testing of a randomly bred population. To circumvent this problem in future publications of this material, the latency scores of each strain will be compared with the scores of subjects from unselected strains which served in previous experiments. For instance, they could be meaningfully compared with the scores of the 40 Day Old group in Experiment 1 (Chapter 5).

SECTION III

GENERAL DISCUSSION

12

HAMSTER PREDATION IN PERSPECTIVE : COMPARATIVE ASPECTS, '

OVERVIEW AND AREAS FOR FUTURE RESEARCH

The aim of this final chapter will be threefold. First, the
discussion will centre on predation in the hamster and the similar-
ities and differences it has with the predatory behaviour of closely
related mammalian species (particularly the rat). Second, an over-
view of the main experimental findings reported in this treatise
will be presented, and last, areas for future research will be
suggested.

12.1. PRINCIPLES OF THE COMPARATIVE APPROACH

Animal psychologists, by tradition, and largely since the
time of Darwin have always had a deep rooted interest in drawing
behavioural parallels between different species within the animal
kingdom. The sub-discipline which arose within psychology in the
first part of the 20th century, that of comparative psychology, is
obviously suggestive of this fact. The early founders of this school
such as G. Romanes, and even the more progressive ones like
J.M. Warren and M.E. Bitterman, often felt content to compare the
behaviour of distantly related species in order to establish general-
ities and principles upon which a science of animal behaviour could

be based. Eventually, it was hoped that with this approach some
sort of phylogenetic scale, based largely on an animal's mental
capacity, or its capacity to learn, would emerge. This traditional
approach, with no genuine theoretical basis (Hodos and Campbell,
1969), was on the whole accepted uncritically by most comparative
psychologists until relatively recently. The reasons for this
acceptance, and its rejection, have been admirably outlined in an
interesting paper by Lockard (1971).

Without going into its details and realizing that Lockard may
be criticized for setting up a 'straw dog', this paper is neverthe-
less important in that it exposed those fallacies present in the
theoretical approach of traditional comparative psychology. While
doing this Lockard also clearly summarized the main tenets of the
approach that 'won - out' - the one encompassed within an evolution-
ary - ecological framework and the one adhered to today by most
contemporary comparative psychologists (Dewsbury and Rethlingshafer,
1973). Briefly we may summarize this position, for it is on this
basis in which we will attempt to put hamster predation in comparative
tive perspective.

According to Lockard the two principles on which a truly com-
parative analysis of animal behaviour can be made are conceptually
simple. First, similar behaviours or behavioural processes in dif-
ferent species may be compared on the basis of phylogenetic relatedness.
This assumes that the species chosen for comparison are descendants
from a common ancestry and therefore should behave in similar fashion.

Behavioural similarities that are found due to common ancestry

are said to be homologous.

The second principle of the comparative approach is what

Lockard terms ecological convergence. This states that similar

behaviours in unrelated species arise from similar selection

pressures from the different niches in which the species have

evolved. Thus those behaviours in distantly related species which

have similar external appearances, or function, are said to be

analogous.

From these two principles four basic types of "strategies

for comparison" emerge (Altmann, 1974). First, the research

worker may compare unrelated species who inhabit dissimilar niches.

This probably is the least informative and most illogical type and

it is the one most prevalent in traditional comparative psychology.

Many examples of this type of comparison could be cited, but perhaps

the most dramatic appears in a paper by Warren (1965) who compared

the behaviour of paradise fish, goldfish, chickens, cats, horses,

raccoons and rhesus monkeys on a spatial discrimination task.

Secondly, unrelated species with similar habitats may be compared.

Similarities that were found, as mentioned above, could be attribu-

ted to ecological pressures. The third and fourth strategies, by

far the most fruitful and illuminating, consist of comparing closely

related species in dissimilar habitats, or similar habitats, respec-

tively. In the case of the former, differences that were found

could be attributed to selection pressures from the environment.

Perhaps the best known study along these lines is the classic

work of E. Cullen (1957) on the adaptation to cliff nesting in

kittiwake gulls. Cullen found that the behaviour of this species,

particularly that associated with breeding, was neatly adapted to

a cliff nesting existence and differed considerably from the breed-

ing habits of closely related ground living gull species. The last

strategy of comparison, that of comparing related species who have

evolved in similar niches is, along with strategy three, an espec-

ially powerful tool for tracing the evolution of behaviour. For

example, by using these two strategies in combination, hypotheses

could be made concerning the phylogenetic age of a given behaviour

(that is, which behaviours have most recently evolved and which,

phylogenetically, are the oldest?).

With this cursory sketch into the logic behind the comparative

method (one should consult Hinde and Tinbergen, 1958 or Hinde, 1970

for a far more sophisticated treatment) we are in a better position

to judge the comparative strategies most suitable for us so that we

can put hamster predation in perspective in a meaningful way. How-

ever, before we begin the reader should realize that the primary

intent of the experiments reported in this treatise was not to make

a comparative analysis of hamster predation _per_ _se_ (if this were the

case then data on the predatory habits of closely related species

within the family Cricetidae, such as __Cricetus__ __cricetus__ or __Cricetulus__

__barabensis__ would have been needed), but rather to elucidate those

mechanisms which affected its ontogeny. Realizing this, then, we

must draw on research by other workers using different species in

order to accomplish this task.

We may ask, then, what species are available for comparison? From the review in Chapter 2 we know that the rat, domestic cat, various marsupial species and some of the larger feral canids and felids have been the most extensively studied mammalian predators. Out of these it would appear that the rat would be the most logical candidate for comparison, for ancestrally it is close to the hamster (both in the Order Rodentia), although the habitat from which it has evolved probably differs in some important respects from the semi desert-like niche of the hamster (hence, a Type III comparison). On the contrary, it could be said that the habitat in which the rat and hamster have most recently evolved is no more than the controlled habitat of the laboratory scientist. Therefore, the habitat of each may be viewed as being identical (hence, a Type IV comparison). Whatever the case, comparison between the rat and hamster would fall under strategy three or four; therefore, comparisons of this sort will be undertaken in Section 12.2.

Further, consider the comparison between the domestic cat and hamster. This would be a Type I comparison; that is, unrelated species which have evolved in dissimilar habitats. The same also holds true if the hamster was compared with the cheetah, the hyena or the African hunting dog. On the other hand, comparing the hamster with one of the smaller marsupial species, such as the marsupial mouse, could conceivably be considered a Type II comparison, for both inhabit similar niches in the wild (e.g. hot, arid type environments). Comparisons of Type II undoubtedly would be helpful; however, it would be premature to make an analysis of this type at

this time, due generally to the paucity of relevant information.
Therefore, scrutiny of this type of comparison will not be under-
taken. Moreover, as mentioned above, comparisons of the first
type yield little in terms of the phylogeny of the response, or
the ecological pressures which may have caused behavioural diver-
gence; hence, theoretically, from an evolutionary viewpoint, they
should be avoided. Thus, along with Type II comparisons, they will
not be considered in the discussion below.

12.2. COMPARATIVE ASPECTS OF STRATEGIES III AND IV

Behavioural Morphology: Behaviourally speaking, both rat
predation and hamster predation are highly similar. Both species
make use of most of their sense modalities to search out, locate
and kill prey. This has been substantiated for the rat (see rele-
vant references in Chapter 2) and for the hamster it has been
suggested by this author in a recently published paper (Polsky,
1974; also see Appendix C). Further, experienced predators of
both species usually consume the prey after they have made a
capture or kill, with eating usually commencing from the anterior
end down.

One important behavioural difference exists, however, between
the two species. This is concerned with the method of killing.
Rats invariably kill their prey, whether it be mice or frogs, with
a bite directed at the nape of the neck (Bernstein and Moyer, 1970).
On the other hand, hamsters show no such orientation, and usually

kill mice (if they do kill them at all - the incidence of spontaneous killing seems to be extremely low) with a number of bites randomly distributed to the body, or by tearing and ripping the flesh with their incisor teeth (Hemmer, 1968; author's personal observations). One could relate these differences in killing techniques to the fact that rats, being much larger than hamsters, have, as predators, adapted mainly to take vertebrate prey, with which a neck bite would be most effective. Hamsters, it could be argued, by contrast, have evolved mainly to take smaller prey of the invertebrate type, such as insects; hence, a neck bite for them would be of no real advantage.

Further ecological studies could bear these points out if, for example, one was to make an analysis of the type of prey taken in the wild through stomach analysis. For the hamster this still needs to be done, and for feral Rattus norvegicus Landry (1970) has summarized much of the evidence which indicates that they prey upon such species as rabbits, frogs and insects. It seems unlikely, though, that Rattus norvegicus takes mice as prey in the wild. Crowcroft (1966) in his extensive studies of wild mouse populations, makes no mention of his subjects falling prey to rats, nor does Barnett (1963) mention it in his well-known text on wild rat behaviour.[1]

1. Karli's assertion "the conflict rat vs. mouse is not an artificial situation created by the experimenter, but a biological phenomenon observed in nature" may be erroneous (see Karli, 1956, p-82).

Ontogeny of the response: Three factors will be considered

under this heading; namely, the age of a predator, its genetic

make-up and the effects of experience within the test situation.

Consider first the last of these. Most of the experiments

reported in this treatise have shown, either indirectly or directly,

that this factor often plays a large role in hamster predation.

Specifically, we found that with experience in the test situation

a hamster's reactivity to the prey usually changed from one extreme

to the other; that is, from ambivalence and withdrawal to capture

and eat. We thus concluded in Chapter 5 that a hamster probably

learnt: 1) that the prey was harmless, 2) that the prey was in

fact edible and palatable and 3) the most efficient means by which

to capture.

For the rat the story seems to be much the same. For example,

we know from the research of Myer and others (see relevant references

in Chapter 2) that rats, when first presented with novel prey often

behave in an ambivalent fashion, thus suggesting that a mouse to a

naive rat is much like a locust to a naive hamster; that is, it

has the potential to induce a response (withdrawal) indicative of

fear. Further, like the hamster, a rat's fear usually attenuates

with increased exposure (to the prey) and that with experience in

killing, rats become more efficient in terms of latency to kill and

in terms of where the killing bite is directed. In addition, like

hamsters, rats often show hesitancy about eating the prey after the

first few kills. So, in general, it seems for both species experience

within the test situation has positive effects on the development

of the predatory response. This then suggests that learning is

the mechanism most responsible for bringing about this change,

although it does not obviate the possibility that rat predation,

like hamster predation, is founded upon certain predispositions

characteristic of the species.

The nature of these predispositions, one must remember, is

not of the kind of 'all or none', but rather is such that a con-

tinuum exists so that any predisposition may be expressed in terms

of a potential. Thus we concluded that all hamsters possessed the

potential to capture, with the potential varying in degree from

individual to individual. That is, some individuals have more

of it than others. And as we know from the review in Chapter 2 this

same conclusion has been expressed by others in regards to rat pred-

ation.

Since any individual may be regarded as having only a potential

to predate, it therefore would be judicious to ask just what the

mechanisms are which control its expression. Many factors could be

regarded as such if one generally views a mechanism as "the thing

which makes behaviour work". Broadly, these could include the various

neurophysiological substrates or the different kinds of experience

encountered by the individual during ontogeny. Some factors concerned

with the latter will be considered shortly, but for now, in the con-

text of the present discussion, the mechanism of genotype seems to

be the most outstanding. To avoid repetition the positive findings

of the selective breeding programme (reported in the previous chapter) will not be reiterated. It would be of interest, though, to compare these findings with those for the rat. Karli, as noted in Chapter 2, failed to find any change in the spontaneous killing reaction of rats exclusively bred for killing. Thus, after a two year period, and contrary to his expectations, he produced no conclusive evidence of a direct genetic influence on mouse killing. However, he did, along with others, find that the incidence of killing induced by an experiential means occasionally depended on the strain of the rat or its sex, thus indicating that genotype may be of some importance.

To this author the negative findings of Karli's breeding programme are perplexing. This perhaps is a par excellence case where negative findings should have been reported in journal form. However, Karli chose to report these findings (at least in English) in about three sentences in a summary paper prepared for a symposium on aggressive behaviour. Knowledge concerning the methodology of Karli's experimental procedures would clarify things considerably, for it may have been that some procedural factor obviated the differences present between the strains. Obvious methodological features which must be considered are, for example, the conditions of housing (alone or with conspecifics?), the duration of a test, the frequency of testing and the size of the testing compartment. In view of these facts, and not knowing if Karli took them into account, additional research on the genetics of rat predation should be undertaken.

Another discrepant finding between rat predation and hamster predation concerns the effects of age. With rats it appears that

this factor is of negligible concern (Myer, 1971) whereas with hamsters the converse seems to hold; that is, it has an unmistakedly strong effect (Experiment 1, Chapter 5). At present no straightforward explanation is available for these findings. Tracing the discrepancy to ecological pressures or social organization would be difficult in light of our present knowledge and it is unlikely that it be explained on an endocrinological or neurological basis. Tentatively, however, one could conjure an explanation in terms of the relative size of the prey to the predator. That is, to some degree, mice are smaller to rats than locusts are to hamsters. Moreover, this relationship seems to hold mainly for the younger animals. To put it in strictly quantitative terms, one could say that an average size juvenile rat is roughly three times the size of its prey (assuming an average size mouse), whereas the ratio of an average size juvenile hamster to a 4th instar locust is not quite as large. If this reasoning is correct, then it fits in well with the hypothesis of Schneirla (1959) which states that the more intense a stimulus is (in this case size being correlated with intensity) the more likely it is to evoke a response of withdrawal rather than approach. And since an animal withdraws, this then is indicative of fear which, as suspected, inhibits the tendency to capture. Thus from this reasoning it could be concluded that younger rats kill with the same incidence as adult rats because they encounter prey of roughly the same size. Younger hamsters, however, are less likely to capture than older hamsters in large part because the prey they face is relatively much larger and therefore more intimidating.

An experiment conducted by this author (not reported in this treatise) supports the contention that the size of the prey in relation to the size of the predator may influence the incidence of capture. In this experiment hamsters were tested at two different ages (30 days and 70 days) with prey of two different sizes; that is, locusts of the 3rd and 5th instar, respectively. The results showed that the younger hamsters captured the smaller prey significantly more frequently than the larger prey, whereas the older hamsters captured the larger prey about as many times as the smaller prey. Further, there was no difference in the incidence with which the smaller prey was captured by the subjects in either age group. These results indicate that some feature of large prey inhibits the tendency to capture in juvenile hamsters. Exactly what this feature is could be the subject of future inquiry. From the discussion above one would probably assume that it is overall size, but it could be, for example, that larger locusts simply move in a different fashion (i.e. crawl faster, hop higher or hop more frequently).

Effects of Food and Water Deprivation: For the rat the relationship between hunger and the likelihood of predation has been discussed in detail in Chapter 2, Section 2.4b.6 (an amended version of this section has recently been published (Polsky, 1975, or see Appendix C). To briefly summarize, the results for the rat point to the conclusion that food deprivation increases the chances of killing in the subject which has had no prior experience with the prey, while on the contrary, depriving an experienced mouse killer of food seems to have very little effect; that is, whether hungry or not experienced killers will kill

if given the opportunity. In addition, other findings indicate
that hunger will not induce killing in non-killers.

In order to examine what effect hunger had on a hamster's
predatory response this author conducted a series of experiments
(these will not be reported in this treatise but they should appear
in journal form in the near future). To summarize the main findings
for the purposes of comparison, it was found that food deprivation
(usually continuous for three days) served as a strong potentiator
for the induction of locust capture in naive subjects. In other
words, when compared to food satiated controls, deprived naive
subjects showed a significantly greater incidence of capture.
Further, other results showed that deprived subjects which captured
continued to capture when food satiated. Thus, like the rat, an
experienced hamster captor will continue to capture whether hungry
or not.

However, for the hamster, and contrary to the findings for
the rat, food deprivation also seems to increase the likelihood
of capture in experienced non-captors. For example, in one experi-
ment established non-captors from the strain of hamsters exclusively
bred for the tendency of non-capture (see Chapter 11) were starved
for three days and then tested. Prior to this they had met the
criterion of failure to capture on three successive occasions.
Compared with controls (i.e. those non-captors who remained on an
ad lib feeding regimen during testing) food deprived subjects showed
a significantly greater incidence of capture.

Another finding which is in apparent conflict with the rat data

concerns the effects of water deprivation. In several experiments

(to be subsequently published) this author found that by depriving

a naive hamster of water for at least three days, the chances of

capture could be increased considerably. It should be recalled

that Paul et al. (1971) found that similar treatment had no apprec-

iable effect on mouse killing by naive rats.

Effects of Social Isolation: The findings concerned with the

effects of this treatment are, for the rat, somewhat equivocal.

However, when frogs are used as prey it is now clear that prior

social isolation increases the likelihood of killing (Johnson et al.

1972). This finding contrasts with the results of a study conducted

by this author in which hamsters were isolated immediately after

weaning and then subsequently tested for locust capture when they

reached approximately 60 days of age. Compared with controls

(i.e. those who were socially reared) isolated subjects showed no

difference in the incidence of capture.

The fact that lack of early conspecific contact has negligible

effects of locust capture by hamsters and positive effects on frog

killing by rats could possibly be traced to the social organization

characteristic of each species. Hamsters, it is widely believed,

live a largely solitary type of existence in the wild, while rats,

as it is well-known, live almost entirely in gregarious social groups

(Barnett, 1963). Therefore, socially isolating a rat from its own

kind for a prolonged period either from weaning or when adult is no

doubt an unnatural experience, and it could be that such treatment produces a general behavioural syndrome not typically found in the socially reared subject. One feature of this syndrome could be increased emotionality or hypersensitivity to external stimuli (Korn and Moyer, 1968). This in turn could be the underlying basis for the increased tendency to kill frogs. The observations of Johnson et al. (1972) are consistent with this interpretation. If this is true then it suggests that frog killing by rats which have undergone a period of isolation is aggression of the irritable type or fear induced type and not of the predatory type (see Moyer, 1968).

Effects of a Novel Environment: It has been amply demonstrated that, for the rat, this factor acts to inhibit both mouse killing and frog killing in the experienced killer. Killing, however, usually re-appears after a period of time, due to the process of habituation. Essentially the same results have been obtained for the hamster (Polsky, 1974, or see Appendix C).

Areas in Need of Comparison: It has been established that:
1) both rats and hamsters kill prey in excess of their food require-
ments; 2) both species kill in the absence of conventional reinforce-
ment (i.e. feeding on the prey); 3) the predatory response of each can be facilitated through prior sensory pre-exposure to the prey; 4) the predatory response of each can be potentiated through prior feed on dead prey; and 5) the predatory response of each can be suppressed through appropriate experiential treatment (in one experi-
ment this author suppressed locust capture by coating the prey with

a 50% solution of quinine hydrochloride). These are other areas

that could have been considered from a comparative viewpoint.

Additional areas of comparison which might prove fruitful when

more data are collected are concerned with the neurophysiology

of predation and the effects of certain kinds of infantile stim-

ulation.

12.3.   CONCLUSIONS AND AREAS FOR FUTURE RESEARCH

One must realize that the paucity of knowledge on hamster

ecology limited to an extent the depth of discussion that could

have been developed in certain parts of this chapter. For example,

no mention was made of why food and water deprivation have a more

pronounced effect on hamster predation than rat predation. This

difference, in part, no doubt probably relates to the feeding

habits of each of these species in the wild; thus it would have

been interesting to have discussed these findings in relation to

these factors. Another good example is the inhibitory effect of a

novel environment. Why exactly should a novel environment exert

its influence in this way? Why not the opposite? What relevance

does this finding have to territoriality and home range behaviour

in feral conditions?

On the other hand, if we assumed that the hamster and rat

came from similar environments, that is, that of the laboratory

scientist, then our discussion would have still been hampered due

to the lack of knowledge concerning the effects of domestication.

We know that this factor has greatly modified many behaviours in the laboratory rat, including its predatory behaviour (Boice, 1973) and whether domestication has affected hamster behaviour as much as it has rat behaviour is still largely unknown.

So far as this author is concerned a greater understanding of hamster ecology, and the effects of domestication, would have permitted a more comprehensive discussion from a biological point of view. Obviously then, without the relevant biological questions asked, our attempt to put hamster predation in comparative perspective from the viewpoint of strategies III or IV might appear, perhaps, to the competent mammalian ethologist, to be somewhat premature or even facile. Nevertheless the attempt was made and the reader should realize the limitations.

However, the reader should not take the above to mean that the questions asked and the design of the experiments reported in this treatise are meaningless - they were in fact very meaningful, but only meaningful from one level of analysis, that of the organismic level (Scott and Bronson, 1964).[2] In other words, it is not absolutely essential for one to have much knowledge about hamster ecology or hamster domestication in order to ask meaningful and pertinent questions about predatory behaviour within the individual. This, as it should be abundantly clear by now, was the primary purpose of the experimental work reported in Section II, with special attention being focused on the ontogeny response.

---

2. Scott and Bronson (1964) identify five levels of behavioural analysis; genetic, physiological, organismic, social and ecological.

Thus, realizing the problems the researcher is confronted with when attempting to put hamster predation in comparative perspective, and further realizing the intent of this treatise, one topic needs mentioning before bringing this final chapter to a close. This, appropriately, will be concerned with the areas to which future studies on hamster predation may direct themselves.

As with any biological phenomenon four basic questions need answering. These have been listed by Tinbergen (1963) as questions concerned with: 1) ontogeny, 2) mechanisms, 3) function, and 4) phylogeny. Working within this framework the questions about hamster predation that could be raised in future investigations are as follows:

1) <u>Questions concerned with ontogeny</u>

Many questions relevant to ontogeny have been raised and answered in the research reported in this treatise. However, for the convenience of the reader, and as a general overview, the main findings will be summarized:

a) Assuming that a hamster is naive, the older it is the more likely it is to capture (Experiment 1, Chapter 5).

b) With experience in the test situation the chances of capture increase and with experience of several successful captures a hamster becomes more skilled and efficient in its capture techniques (Experiment 1, Chapter 5).

c) Most hamsters, immediately following capture, will consume the prey in its entirety; younger hamsters, however, may abandon the prey after the first few captures (Experiment 1, Chapter 5).

d) Hamsters as young as 20 days will capture and consume the prey in the normal adult manner (Experiment 2, Chapter 6).

e) If naive hamsters are administered several successive tests for locust capture then the chances of capture are more likely to increase significantly with repeated testing if the ITI is 5 or 10 days rather than 1 day (Experiment 3, Chapter 7).

f) Prey removal after capture decreases the chances of capture in relatively inexperienced subjects (Experiment 4a, Chapter 8). However, prey removal from established captors has negligible effects (unreported findings). Further, eat does not have to immediately follow capture in order to strengthen the tendency to capture (Experiment 4b, Chapter 8). Lastly, the capture response in hamsters with weak dispositions to capture can become extinguished by removing the prey after capture; this same treatment has virtually no effect on hamsters with a strong disposition to capture (Experiment 4c, Chapter 8).

g) Feeding dead prey to naive subjects of at least 30 days of age increases the chances of capture (Experiment 4a, Experiment 4b, Chapter 8; Experiment 5b, Chapter 9). On the other hand, feeding dead prey to hamsters prior to weaning has no appreciable effect on later capture tendency (Experiment 5a, Chapter 9). Further, prior feeding on eviscerated prey seems to be as advantageous (i.e. for an

increased capture tendency) to the naive subject as prior feed on

dead whole prey (Experiment 5c, Chapter 9).

h) A naive hamster's predatory response can be 'primed' through

prior sensory exposure (to the prey) via the olfactory and visual

sense modalities (Experiment 6a, Chapter 10). However, in order for

priming to be most effective a hamster must be approximately 45 days

of age. Priming the predatory response of hamsters younger than this

(approximately 30 days of age) is ineffective (Experiment 6b, Chapter

10).

i) Two strains of hamster were selectively bred for the oppos-

ite tendencies; that is, the tendency for capture (Captors) and the

tendency for non-capture (Non-Captors).

Several questions which still need answering from the viewpoint

of ontogeny are as follows:

1) What are effects of early infantile stimulation (e.g.

electric shock, cooling, handling) ? What are the effects of the

early maternal environment ?

2) In what ways do experiential factors interact with the

genotype of the individual ?

3) What are the effects of observational learning ? Can

non-captors be induced to capture if they were allowed to observe

an experienced conspecific make capture ? Can the predatory response

be socially facilitated ?

2) Questions concerned with mechanisms

Here the questions centre around the short term causes of predation. As such, questions about mechanisms may be broadly stated in either exogenous or endogenous terms.

Exogenous questions would be concerned with, for example:

a) The specific stimuli from the prey needed to trigger the stereotyped response of capture. Are some stimuli more important than others (for instance, movement) or do they act in a cumulative fashion? Further, what stimuli bring about the initiation of eating? Are they different from those for capture? As an adjunct to an investigation of this sort, the researcher could make a detailed inquiry into the sense modalities used for capture. For instance, it would be interesting to know if centrally and peripherally induced types of anosmia exerted similar effects.

b) The effects of aversive stimuli when in the presence of prey. Will electric foot shock induce the response of capture? Will a sub-lethal dose of lithium chloride administered after capture suppress subsequent capturing?

Endogenous questions would be concerned with, for example:

a) The neurophysiological mechanisms in control of the predatory response. Are unique centres present in the brain which when stimulated, either electrically or chemically, will elicit this

behaviour? If so, how does such stimulation vary with the charac-
teristics of the prey, the environment in which the test takes place
or with the animal's past experience?

b) Further, will such stimulation elicit the predatory res-
ponse in established non-captors?

3) Questions concerned with function

Obviously we know that functionally for the individual, the
capture of prey serves as a means of acquiring food. But could it
also serve a social funtion among conspecifics? For example, if
given the opportunity in controlled conditions, would a hamster
mother introduce prey to her newborn pups? If so, then what function
would this serve? Secondly, in a social group, would only the most
dominant capture? If so, then what function would this serve?
Thirdly, will the members of a captive social group pass on prey to
conspecifics? If so, then what function would this serve?

4) Questions concerned with phylogeny

Questions from this angle are perhaps the most difficult and
challenging to answer. As stated previously, the researcher when
attempting to answer evolutionary questions must compare ancestrally
related hamster species and look for predatory differences either in
terms of causality, ontogeny, mechanisms or function. If differences
were found, then the question is simply what can the differences be
attributed to? In other words, what selection pressures, social or

environmental, were responsible for behavioural divergence ?   At

this stage with our limited knowledge about the predatory habits

of other hamster species, and on hamster ecology per se, questions

like these can only be viewed as projects for future research

endeavours. The point then, for the serious hamster researcher,

is to go into the fields of Aleppo in order to gather as much

information as possible on hamster ecology and its relationship

to hamster behaviour. Until then, theories concerned with the

evolution of hamster predatory behaviour will certainly be welcomed,

but nevertheless must be treated with caution.

APPENDIXES

CONTENTS

APPENDIX C

Published Papers

Effects of Novel Environment on Predatory Behaviour of
Golden Hamsters.

Hunger, Prey Feeding and Predatory Aggression.

APPENDIX D

Further Reading

APPENDIX A

405.

APPENDIX A

Table 1. Major variables of study and their effect on mammalian predatory behaviour.[a]

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Early Isolation	Kuo, 1960	Facilitory	Cats/Dogs	Birds and rodents
	Myer, 1969	Negligible	Rats	Mice
	Johnson, et al., 1970, 1972	Facilitory	Rats	Frogs
Adult Isolation	Pion, 1969; Bernstein and Moyer, 1970	Facilitory	Rats	Mice
Early Exposure to the Prey	Kuo, 1930	Inhibitory	Cats	Rats and mice
	Kuo, 1960	Inhibitory	Cats/Dogs	Birds and rodents
	Denenberg. et al., 1968; Myer, 1969	Inhibitory	Rats	Mice
	Galef, 1970	Inhibitory	Wild rats	Mice
	Johnson, et al., 1972.	Facilitory	Rats	Frogs
	Johnson, et al., 1972.	Negligible	Rats	Cockroaches
Infantile Handling	Galef, 1970	Negligible	Wild rats	Mice
Witnessing a Kill	Kuo, 1930	Facilitory	Cats (non-killers and adults)	

Table 1, continued.

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Witnessing a Kill	Kuo, 1930	Negligible	Cats (with previous prey contact)	Rats/Mice
	Pion, 1969	Facilitory	Rats(naive)	Mice
	Johnson, et al., 1972	Facilitory	Rats(non-killers)	Frogs
Age of Predator	Myer, 1971	Negligible	Rats	Mice
Social Competition	Kuo, 1960	Facilitory	Cats/Dogs	Birds and rodents
	Heimstra & Newton, 1961	Facilitory	Rats	Mice
	Whalen & Fehr, 1964	Negligible	Rats	Mice
	Heimstra, 1965	Facilitory	Rats	Mice
Electric Shock[b]				
Contingent	Myer, 1966a, 1966b, 1967, 1968. Baenninger, 1967, 1970	Inhibitory	Rats (experienced killers)	Mice
	Kuo, 1930	Inhibitory	Cats	Rats/Mice
Non-Contingent	Baenninger & Ulm, 1969; Myer & Baenninger, 1966	Facilitory	Rats (supressed killers)	Mice
	Karli, 1956; Myer & Baenninger, 1966	Negligible	Rats(non-killers)	Mice

Table 1, continued.

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Electric Shock[b]				
Non-Contingent	Ulrich, et al, 1964	Facilitory	Cats	Mice
	Clark, 1962	Facilitory	Grasshopper Mice	Domestic mice
Novel Environment				
	Karli, 1956	Inhibitory	Wild rats	Mice
	DeSisto & Huston, 1970	Inhibitory	Rats	Frogs
Castration				
Early	Baenninger & Miley, 1971	Inhibitory	Rats	Mice
Late	Karli, 1958	Negligible	Rats	Mice
Genotype				
	Thomas, 1969,1972	Yes	Mice	Crickets
	Karli, et al.,1967; Flandera & Novakova, 1971	Negligible	Rats	Mice
Strain X Sex	Paul, et al., 1971	Yes	Rats	Mice
Strain X Bulbectomy	Karli, et al., 1969; Thorne, et al., 1973	Yes	Rats	Mice
Strain X Food Deprivation	Paul, et al., 1971	Yes	Rats	Mice

Table 1, continued.

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Rank in Dominance Hier-archy	Leyhausen, 1973	yes.	several species of felid	Rats
	Clark, 1962a	yes	Grasshopper mice	Domestic mice
	Karli, et al., 1969		Rats	Mice
	DeSisto & Huston, 1970	yes	Rats	Frogs
Gestation, Lactation, etc.	Karli, 1956; Baenninger, 1969	Negligible	Rats (non-killers)	Mice
	Baenninger, 1969	Negligible	Rats(killers)	Mice
	Flandera & Novakova, 1971	Facilitory	Rats (Wistar-SPF strain)	Mice
	Endroczi, et al., 1958	Facilitory	Rats	Frogs
	Revlis & Moyer, 1969	Negligible	Rats	Frogs
Sex of Predator	Karli, 1956; Bernstein & Moyer, 1970; Lonowski, et al., 1973	Negligible	Rats	Mice
Feed on Prey Subsequent to Kill	Karli, 1956; Myer, 1964, and many others	Negligible	Rats	Mice
Prior Feed on Dead Prey	Paul, 1972; Paul & Posner, 1973	Facilitory	Rats	Mice

Table 1, continued.

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Food Deprivation				
Continuous	Karli, 1956	Negligible	Rats(non-killers)	Mice
	Paul, 1972	Facilitory	Rats(naive)	Mice
Cyclic	Whalen & Fehr, 1964; Paul,et al., 1971.	Facilitory	Rats(naive)	Mice
Olfactory Bulb Lesions	Alberts & Friedman, 1972; Spector & Hull, 1972, and several others.	Facilitory	Rats(non-killers)	Mice
	Bandler & Chi, 1972	Inhibitory	Rats	Frogs & Mice
Zinc Sulphate Induced Anosmia	Alberts & Friedman, 1972	Negligible	Rats(non-killers)	Mice
Hypothalamic Stimulation				
Electrical	Panksepp, 1972; King & Hoebel,1968; Vergnes & Karli, 1969, 1970.	Facilitory	Rats(non-killers)	Mice
	Vergnes & Karli, 1969	Facilitory	Rats (killers)	Mice
	Wasman & Flynn, 1962; Roberts & Kiss, 1964, and many others	Facilitory	Cats(non-killers)	Rats

Table 1, continued.

VARIABLE	INVESTIGATOR & DATE	EFFECT	PREDATOR	PREY
Hypothalamic Stimulation				
Electrical	Roberts, et al., 1967	Facilitory	Opossums	Rats
Chemical	Bandler, 1969; Smith, et al., 1970	Facilitory	Rats(non-killers)	Mice
Lesions in the Limbic System	Malick, 1970; Panksepp, 1971b; Miczek & Grossman, 1972.	Facilitory	Rats(non-killers)	Mice
Successive Removal of Sense Modalities	Karli, 1961; Myer, 1964	Negligible	Rats(killers)	Mice

a In the majority of cases the variables listed either facilitate, inhibit, or have negligible effects on the predatory response. In some cases, however, a 'yes' is indicated; this should be taken to mean that the variable(s) in question has been found to have only an association with the incidence of prey-killing and therefore should not be regarded as having a causal effect.

b Contingent shocks refer to shocks administered at the time of attack and non-contingent shocks refer to shocks uncorrelated with attack.

APPENDIX B

Table 1. Raw latency to capture in Experiment 1 (Chapter 5); The Influence of Age and Experience. Latency scores are in seconds.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	300	158	300	300	300	300	300	81	300	300	300	300
2	300	37	300	300	300	300	300	99	300	300	300	300
3	300	58	209	300	137	300	300	69	300	300	300	300
4	300	51	116	300	54	300	300	52	300	44	166	300
5	300	70	71	300	231	44	300	52	300	48	29	300
6	300	52	40	300	58	83	300	40	88	25	35	300

30 Day Old (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	300	286	300	300	300	190	268	300	300	300	300
2	300	300	300	300	300	40	55	300	300	300	300
3	300	62	299	300	139	41	48	300	300	300	300
4	300	145	183	300	148	37	48	300	300	300	300
5	300	41	83	300	75	33	116	300	300	300	300
6	300	53	109	300	300	36	44	300	300	300	300

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	300	300	218	300	270	300	143	300	300	158	300	64	300
2	180	300	298	300	300	300	54	110	300	48	300	15	31
3	300	300	186	300	52	300	241	300	300	71	300	16	33
4	72	300	31	300	53	300	54	36	136	33	69	10	23
5	33	300	133	300	73	300	15	98	300	26	44	14	20
6	48	300	71	300	34	33	27	54	300	10	33	17	22

Table 1, continued.

40 Day Old (con't).

	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	300	300	300	55	300	300	300	300	300	300	136	300	300
2	225	300	300	183	300	300	300	300	145	244	43	36	33
3	47	300	242	35	300	236	300	300	48	148	19	29	22
4	76	147	140	82	300	85	300	300	42	32	14	28	28
5	35	78	32	40	300	37	300	293	41	21	10	21	23
6	85	207	189	41	300	229	300	300	25	30	12	27	24

SESSION (rows)

50 DAY OLD

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	300	300	245	300	161	300	299	146	123	137	300	300	300	300
2	300	300	44	300	50	300	119	60	300	83	300	300	300	300
3	300	64	61	300	16	300	81	40	165	81	300	60	300	300
4	136	90	31	300	30	300	50	32	186	32	300	104	300	43
5	75	87	32	170	14	300	105	45	162	31	300	73	300	23
6	66	238	39	57	21	300	93	62	36	52	300	74	300	36

SESSION (rows)

50 Day Old (con't).

	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	300	150	64	136	300	39	300	209	300	300
2	300	37	36	77	300	22	300	57	206	300
3	74	55	29	32	300	13	300	25	33	300
4	50	64	45	62	300	20	300	25	40	300
5	39	26	22	27	300	10	300	44	40	300
6	31	24	22	35	300	9	300	31	16	40

SESSION (rows)

Table 1, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	300	47	300	32	29	64	69	67	78	35
2	300	34	300	44	24	54	287	59	58	27
3	300	24	300	33	11	17	30	77	33	28
4	57	76	300	28	15	14	27	16	19	32
5	30	13	300	30	48	39	47	8	26	19
6	45	30	185	25	11	9	30	18	20	19

(SESSION)

90 Day Old (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	300	300	48	300	81	110	61	32	25	38
2	300	300	28	300	32	28	36	31	24	24
3	300	300	14	300	43	24	63	25	13	29
4	300	300	51	300	58	10	29	25	19	32
5	293	300	33	300	44	10	44	24	16	22
6	300	282	20	300	21	32	300	23	30	35

(SESSION)

Table 2. Raw frequency of exploration in Experiment 1
(Chapter 5); The Influence of Age and Experience.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	10	20	18	5	16	4	0	7	24	29	15	22
2	1	2	16	6	18	13	5	6	16	9	15	22
3	14	7	6	6	15	8	8	3	22	5	9	11
4	14	3	7	13	5	6	7	1	6	4	7	19
5	9	3	4	13	11	1	12	8	5	5	1	10
6	6	3	3	8	6	4	3	3	3	3	5	8

30 Day Old (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	10	22	23	13	36	16	15	8	24	6	16
2	4	7	17	7	19	4	7	23	9	6	10
3	4	4	16	5	12	2	5	17	7	4	15
4	3	9	15	5	8	4	8	16	4	10	5
5	4	3	10	4	2	1	16	11	2	6	5
6	5	4	10	4	19	1	2	11	5	9	18

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	17	16	9	2	13	7	7	28	5	8	15	10	21
2	17	3	14	1	5	4	6	12	14	4	8	1	3
3	17	9	12	1	5	11	28	13	7	3	24	1	1
4	4	3	1	2	3	3	9	7	12	3	8	1	2
5	1	10	8	5	6	2	2	4	6	2	6	2.	1
6	5	13	4	4	2	2	1	7	7	1	5	2	2

Table 2, continued.

40 Day Old (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	28	17	3	4	10	22	11	5	7	11	14	25	5
2	21	7	1	12	7	10	8	5	19	27	2	4	3
3	3	13	13	1	5	8	2	6	7	14	2	1	2
4	3	11	2	7	4	4	9	5	4	7	1	3	7
5	3	3	1	1	1	2	2	20	4	3	2	3	4
6	3	12	4	2	2	9	3	4	1	6	1	4	1

50 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	6	8	17	18	4	7	38	18	12	15	16	11	20	18
2	4	18	4	24	4	10	13	3	4	4	4	34	10	8
3	14	4	6	10	1	6	7	1	9	4	1	5	5	20
4	6	2	1	2	2	12	3	3	6	3	5	11	14	4
5	6	5	1	20	1	6	14	1	1	1	10	5	19	5
6	6	7	1	4	3	5	6	2	4	5	10	5	17	5

50 Day Old (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	13	9	3	13	7	3	9	15	22	15
2	10	1	2	3	7	2	4	8	17	6
3	4	2	2	1	8	1	4	4	4	9
4	2	3	5	3	10	3	1	2	6	7
5	2	1	2	1	3	1	7	6	8	1
6	3	2	2	2	17	1	3	2	2	8

Table 2, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	12	5	20	2	2	8	6	4	8	2
2	16	3	5	3	1	2	14	1	5	1
3	4	2	2	1	1	2	2	1	5	3
4	5	1	15	2	1	1	1	1	1	3
5	2	1	5	1	2	1	3	1	2	1
6	3	5	14	1	1	1	1	1	1	1

SESSION

90 Day Old (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	15	9	6	5	6	11	3	2	3	2
2	15	6	5	3	1	2	3	3	2	2
3	9	9	1	4	1	1	5	1	2	1
4	7	11	3	4	3	1	2	4	1	1
5	21	14	2	5	2	1	2	1	1	1
6	11	12	2	2	1	1	4	1	1	1

SESSION

Table 3. Raw frequency of withdrawal in Experiment 1 (Chapter 5); The Influence of Age and Experience.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	11	9	10	4	9	4	0	1	13	9	1	5
2	1	0	8	5	6	3	4	0	7	2	2	2
3	12	1	3	5	4	5	4	0	9	2	3	4
4	5	0	2	5	1	0	7	0	4	0	0	2
5	2	0	1	5	4	0	6	0	0	1	0	2
6	2	0	0	4	0	1	2	1	0	0	0	1

30 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	10	13	12	8	11	8	5	4	7	3	7
2	4	8	6	5	11	3	3	9	0	1	3
3	3	0	2	4	4	0	3	6	1	1	7
4	1	3	1	2	2	0	1	7	1	6	2
5	3	2	4	2	2	0	8	3	1	1	2
6	3	0	2	1	16	0	0	5	0	2	5

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	9	7	2	0	3	1	2	7	2	3	6	0	1
2	10	2	3	2	0	0	1	0	5	0	1	0	0
3	9	5	2	0	0	3	9	0	1	0	4	0	0
4	1	1	0	1	1	0	2	1	0	0	0	0	0
5	0	4	1	0	0	0	0	0	4	0	1	0	0
6	3	0	2	0	0	0	0	1	2	0	2	0	0

Table 3, continued.

40 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	18	14	4	0	8	18	4	3	3	4	2	7	1
2	8	5	1	0	7	5	3	3	7	7	0	0	0
3	1	7	5	0	5	2	2	3	1	2	0	0	0
4	2	4	0	0	5	0	3	3	0	0	0	0	0
5	0	2	1	0	0	0	0	12	0	0	0	0	0
6	0	6	0	0	4	3	2	2	0	2	0	0	0

50 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	3	6	7	16	0	3	8	5	5	2	3	4	2	8
2	2	3	0	12	0	5	0	0	0	0	0	3	1	3
3	5	0	0	6	0	3	4	0	0	0	0	0	0	8
4	0	0	0	2	0	2	0	0	1	0	2	4	5	1
5	0	0	0	10	0	3	2	0	0	0	1	1	0	1
6	1	0	0	1	0	2	1	0	1	0	4	1	1	1

50 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	5	3	0	1	1	0	5	5	12	7
2	3	0	0	0	4	0	4	0	4	3
3	0	0	0	1	3	0	1	0	0	1
4	0	0	0	3	6	0	2	0	0	2
5	0	0	0	0	2	0	4	1	1	1
6	0	0	0	0	2	0	0	1	1	0

Table 3, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	0	0	2	1	0	2	2	3	0	0
2	1	0	0	0	0	0	5	0	1	0
3	1	0	1	0	0	0	0	0	0	0
4	0	0	1	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0
6	0	0	1	0	0	0	0	0	0	0

SESSION

90 DAY OLD (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	1	5	0	3	1	0	0	0	0	0
2	1	0	0	2	0	0	0	0	0	0
3	2	0	0	3	0	0	0	0	0	0
4	0	0	0	1	0	0	0	0	0	0
5	1	0	0	3	0	0	0	0	0	0
6	5	4	0	2	0	0	0	0	0	0

SESSION

Table 4. Raw frequency of nip in Experiment 1 (Chapter 5);
The Influence of Age and Experience.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M.4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	0	17	2	0	2	0	0	6	5	21	0	0
2	0	1	12	0	0	0	0	3	4	0	0	0
3	0	6	2	0	15	0	0	3	0	0	0	0
4	0	2	7	2	4	3	0	1	0	3	3	0
5	0	2	4	2	5	1	0	1	0	3	1	0
6	0	1	3	0	4	3	0	1	3	2	5	0

30 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F.10	F 11	F 12	F 13
1	0	21	9	1	1	10	5	0	1	0	0
2	0	0	12	0	15	1	2	0	0	0	0
3	0	4	5	0	5	1	3	2	0	0	0
4	0	7	5	0	4	3	5	0	0	0	0
5	0	2	5	0	5	1	6	0	0	0	0
6	0	2	10	0	1	1	1	2	0	0	2

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	3	0	7	0	7	1	3	16	0	5	0	8	0
2	8	0	9	0	1	0	6	11	0	4	0	1	3
3	5	0	7	0	5	1	8	5	0	3	1	1	1
4	3	0	1	0	1	0	2	7	5	3	7	1	2
5	1	0	5	0	3	0	2	3	0	2	5	2	1
6	3	0	1	0	1	2	1	5	0	1	3	1	1

Table 4, continued.

40 DAY OLD (con't).

	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	3	1	1	4	0	0	0	0	0	0	4	15	0
2	6	0	0	11	0	0	0	0	7	12	1	3	3
3	1	0	5	1	0	6	0	0	6	5	2	1	2
4	1	7	3	6	0	1	0	0	4	6	1	3	2
5	3	3	3	1	0	2	0	9	4	2	1	2	2
6	3	6	4	2	0	2	0	3	1	3	1	1	1

(SESSION — rows)

50 DAY OLD

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	0	0	10	1	1	0	7	4	4	8	0	0	0	1
2	0	0	4	3	2	1	8	3	0	3	0	0	0	0
3	0	3	3	0	1	0	2	1	1	4	0	1	0	2
4	3	1	1	0	2	0	3	1	1	2	0	3	0	5
5	5	2	1	8	1	0	2	1	1	1	0	4	2	5
6	4	1	1	3	1	0	1	1	2	5	0	3	0	4

(SESSION — rows)

50 DAY OLD (con't).

	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	0	3	2	6	0	2	0	3	2	0
2	1	1	2	2	0	2	0	8	7	0
3	3	1	1	1	0	1	0	4	4	0
4	2	3	1	3	0	1	0	2	5	0
5	2	1	1	1	0	1	0	6	7	0
6	3	2	2	2	0	1	0	2	1	8

(SESSION — rows)

Table 4, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	4	4	0	1	1	5	3	2	6	2
2	5	3	0	3	1	3	3	1	5	1
3	0	1	0	1	1	2	1	1	1	1
4	4	1	3	2	1	1	1	1	1	3
5	2	1	0	1	2	1	3	1	1	1
6	1	5	9	1	1	1	1	1	1	1

SESSION (for the left side label)

90 DAY OLD (con't)

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	5	0	6	0	5	11	3	2	3	2
2	1	0	5	0	1	2	3	3	2	2
3	0	0	1	1	1	1	4	1	1	1
4	1	0	3	0	2	1	1	2	1	1
5	5	0	2	0	2	1	1	1	1	1
6	1	6	2	0	1	1	4	2	1	1

SESSION

Table 5. Raw frequency of unsuccessful capture in Experiment 1 (Chapter 5); The Influence of Age and Experience.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	0	4	0	0	0	0	0	4	0	2	0	0
2	0	2	16	0	0	0	0	1	0	0	0	0
3	0	3	4	0	7	1	0	2	0	0	0	0
4	0	0	4	1	2	5	0	0	0	1	1	0
5	0	3	4	0	1	1	0	0	0	0	0	0
6	0	4	0	0	2	5	0	0	2	0	1	0

30 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	0	7	0	0	0	5	3	0	0	0	0
2	0	0	11	0	2	1	2	0	0	0	0
3	0	2	6	0	5	2	2	0	0	0	0
4	0	5	7	0	0	0	2	0	0	0	0
5	0	1	3	0	5	1	1	0	0	0	0
6	0	1	5	0	0	0	0	0	0	0	0

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	0	0	5	0	2	1	5	9	0	6	0	1	0
2	4	0	7	0	0	0	6	4	0	2	0	0	0
3	0	0	4	0	1	0	2	13	0	3	0	0	0
4	1	0	0	0	1	0	2	2	4	0	1	0	0
5	1	0	4	0	1	0	0	1	0	0	2	0	0
6	0	0	1	0	0	0	1	2	0	0	0	0	0

Table 5, continued.

40 DAY OLD (con't).

SESSION

	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	0	0	0	4	0	0	0	0	0	0	0	1	0
2	5	0	0	11	0	0	0	0	3	0	0	0	0
3	0	0	5	1	0	2	0	0	1	1	1	0	1
4	3	5	2	6	0	1	0	0	1	0	0	2	1
5	3	5	0	1	0	2	0	1	1	0	0	0	0
6	3	3	9	1	0	0	0	1	1	0	0	0	0

50 DAY OLD

SUBJECT

SESSION

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	0	0	3	0	0	0	5	3	1	2	0	0	0	0
2	0	0	0	0	1	0	8	2	0	0	0	0	0	0
3	0	2	0	0	1	0	2	1	1	4	0	0	0	2
4	3	0	0	0	2	0	2	1	0	1	0	0	0	2
5	2	2	0	1	1	0	1	1	0	0	0	2	0	1
6	3	1	0	3	0	0	0	1	0	5	0	0	0	2

50 DAY OLD (con't).

SESSION

	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	0	1	0	2	0	1	0	1	0	0
2	0	0	0	0	0	1	0	1	3	0
3	1	0	0	1	0	0	0	1	1	0
4	1	3	1	3	0	0	0	0	0	0
5	1	0	0	0	0	0	0	4	1	0
6	1	0	0	1	0	0	0	1	0	1

Table 5, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	0	1	0	0	0	3	1	1	4	1
2	3	0	0	0	0	1	0	0	1	0
3	0	0	0	1	0	0	0	0	0	1
4	0	0	0	2	0	0	0	0	0	1
5	1	0	0	1	0	0	2	0	0	0
6	0	0	0	0	0	0	0	0	0	0

SESSION

90 DAY OLD (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	1	0	6	0	2	1	1	0	0	1
2	0	0	1	0	1	0	0	2	0	0
3	0	0	0	0	0	0	0	0	0	0
4	0	0	2	0	1	0	0	0	0	0
5	1	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	1	1	1	0	0

SESSION

Table 6. Incidence of capture and carry in Experiment 1 (Chapter 5); The Influence of Age and Experience.[a]

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	–	N	–	–	–	–	–	N	–	–	–	–
2	–	N	–	–	–	–	–	Y	–	–	–	–
3	–	N	N	–	Y	–	–	N	–	–	–	–
4	–	N	N	–	N	–	–	N	–	N	N	–
5	–	N	Y	–	N	N	–	N	–	N	N	–
6	–	N	Y	–	N	Y	–	N	N	N	N	–

30 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	–	N	–	–	–	N	N	–	–	–	–
2	–	–	–	–	–	N	Y	–	–	–	–
3	–	N	N	–	Y	N	Y	–	–	–	–
4	–	N	Y	–	Y	N	Y	–	–	–	–
5	–	N	Y	–	N	Y	Y	–	–	–	–
6	–	Y	Y	–	–	Y	Y	–	–	–	–

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	–	–	N	–	N	–	N	–	–	N	–	N	–
2	N	–	N	–	–	–	N	N	–	N	–	N	N
3	–	–	Y	–	N	–	N	–	–	N	–	N	N
4	N	–	Y	–	N	–	N	Y	N	N	N	N	N
5	N	–	Y	–	N	–	N	N	–	N	Y	N	N
6	N	–	Y	–	N	N	N	N	–	N	Y	N	N

[a] Dash (–) indicates no capture
N indicates capture without carry
Y indicates capture followed by carry

Table 6, continued.

40 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	-	-	-	N	-	-	-	-	-	-	Y	-	-
2	N	-	-	N	-	-	-	-	N	N	Y	N	N
3	N	-	-	Y	-	N	-	-	Y	N	N	N	N
4	N	N	N	Y	-	N	-	-	N	N	N	N	N
5	N	N	N	Y	-	N	-	N	Y	Y	N	N	N
6	N	N	N	N	-	Y	-	-	N	N	N	Y	N

50 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	-	-	N	-	N	-	N	N	N	N	-	-	-	-
2	-	-	N	-	N	-	N	N	-	N	-	-	-	-
3	-	-	N	-	N	-	Y	N	N	Y	-	N	-	-
4	N	N	N	-	N	-	N	N	N	N	-	N	-	N
5	N	N	N	Y	N	-	N	N	N	Y	-	N	-	N
6	N	Y	N	N	N	-	N	N	N	N	-	N	-	N

50 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	-	N	N	N	-	N	-	N	-	-
2	-	N	Y	N	-	N	-	N	N	-
3	N	N	N	N	-	N	-	N	N	-
4	N	N	N	N	-	N	-	Y	N	-
5	N	N	N	N	-	N	-	Y	N	-
6	N	N	N	Y	-	N	-	Y	N	N

Table 6, continued.

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	-	N	-	N	N	N	N	N	N	N
2	-	N	-	Y	N	N	N	N	N	N
3	-	N	-	Y	N	N	N	N	N	N
4	N	N	-	N	N	N	Y	N	N	N
5	N	N	-	N	N	Y	N	N	N	N
6	N	N	-	N	N	N	Y	N	N	N

SESSION

90 DAY OLD (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	-	-	N	-	N	N	N	N	N	N
2	-	-	N	-	N	N	N	N	N	Y
3	-	-	N	-	N	N	N	N	N	N
4	-	-	Y	-	N	N	N	Y	N	N
5	N	-	Y	-	N	N	N	N	N	N
6	-	N	Y	-	N	N	-	N	N	N

SESSION

Table 7. The amount of prey eaten on the initial and final capture in Experiment 1 (Chapter 5); The Influence of Age and Experience. Only those subjects which captured on two occasions are included.

30 DAY OLD

SUBJECT

SUBJECT	M 2	M 3	M 6	M 7	M 9	M 11	M 13	F 2	F 3	F 7	F 8	F 9
Amt. eaten on initial cap.	.75	.50	.25	.25	.50	1	.50	.25	.50	.75	.25	.50
Amt. eaten on final capture	1	1	1	.75	1	1	1	1	1	1	1	1

40 DAY OLD

SUBJECT

SUBJECT	M 1	M 3	M 5	M 7	M 8	M 10	M 12	M 13	M 14
Amt. eaten on initial cap.	1	.75	1	.50	.25	.25	1	1	1
Amt. eaten on final capture	1	1	1	1	.25	1	1	1	1

40 DAY OLD (con't).

SUBJECT	F 1	F 2	F 3	F 4	F 6	F 10	F 11	F 12	F13	F 14
Amt. eaten on initial cap.	1	1	.50	.50	.50	.75	1	.50	1	1
Amt. eaten on final capture	1	1	1	1	1	1	1	1	1	1

Table 7, continued.

50 DAY OLD

SUBJECT

SUBJECT	M 1	M 2	M 3	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
Amt. eaten on initial cap.	.50	.75	1	1	.75	1	.75	.75	.25	1	1
Amt. eaten on final capture	1	1	1	1	1	1	1	.25	1	1	1

50 DAY OLD (con't).

SUBJECT	F 1	F 2	F 3	F 4	F 7	F 11	F 12
Amt. eaten on initial cap.	1	1	.75	.50	1	1	.75
Amt eaten on final capture	1	1	1	1	1	1	1

90 DAY OLD

SUBJECT

SUBJECT	M 1	M 2	M 5	M 7	M 8	M 9	M 10	M 12	M 14
Amt. eaten on initial cap.	1	1	1	1	1	1	1	1	1
Amt. eaten on final capture	1	1	1	1	1	1	1	1	1

90 DAY OLD (con't).

SUBJECT	F 6	F 8	F 9	F 10	F 11	F 12	F 14
Amt. eaten on initial cap.	1	.50	1	1	1	1	1
Amt. eaten on final capture	1	1	1	1	1	1	1

Table 8. Incidence of pouch after capture in Experiment 1 (Chapter 5); The Influence of Age and Experience. Dash (-) indicates no capture; N indicates capture without pouch; Y indicates capture followed by pouch.

30 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
1	-	N	-	-	-	-	-	N	-	-	-	-
2	-	N	-	-	-	-	-	N	-	-	-	-
3	-	N	N	-	N	-	-	N	-	-	-	-
4	-	N	N	-	N	-	-	N	-	N	N	-
5	-	N	N	-	N	N	-	N	-	N	N	-
6	-	N	N	-	N	N	-	N	N	N	N	-

30 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
1	-	N	-	-	-	N	N	-	-	-	-
2	-	-	-	-	-	N	N	-	-	-	-
3	-	N	N	-	N	N	N	-	-	-	-
4	-	N	N	-	N	N	N	-	-	-	-
5	-	N	N	-	N	N	N	-	-	-	-
6	-	N	N	-	-	N	N	-	-	-	-

Table 8, continued.

40 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
1	-	-	N	-	N	-	N	-	-	N	-	N	-
2	N	-	N	-	-	-	N	N	-	N	-	Y	Y
3	-	-	N	-	N	-	N	-	-	N	-	Y	N
4	N	-	N	-	N	-	N	N	N	Y	N	Y	Y
5	N	-	N	-	N	-	Y	N	-	Y	N	Y	N
6	N	-	N	-	N	-	N	N	-	Y	N	Y	Y

40 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
1	-	-	-	N	-	-	-	-	-	-	N	-	-
2	N	-	-	N	-	-	-	-	N	N	N	N	N
3	N	-	-	N	-	N	-	-	N	N	Y	N	N
4	N	N	N	N	-	N	-	-	N	N	Y	N	Y
5	N	N	N	N	-	N	-	N	N	Y	Y	N	Y
6	N	N	N	N	-	N	-	-	N	N	Y	N	N

Table 8, continued.

50 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
1	-	-	N	-	N	-	N	N	N	N	-	-	-	-
2	-	-	N	-	N	-	N	N	-	N	-	-	-	-
3	-	-	N	-	Y	-	N	N	N	N	-	N	-	-
4	N	N	N	-	N	-	N	Y	N	Y	-	N	-	N
5	N	N	N	N	Y	-	N	N	N	N	-	N	-	N
6	N	N	N	N	Y	-	N	N	N	N	-	N	-	N

50 DAY OLD (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
1	-	N	N	N	-	N	-	N	-	-
2	-	N	N	N	-	Y	-	N	N	-
3	N	N	N	N	-	Y	-	N	N	-
4	N	N	N	N	-	Y	-	N	N	-
5	N	Y	N	N	-	Y	-	N	N	-
6	N	Y	N	N	-	Y	-	N	N	N

Table 8, continued.

90 DAY OLD

SUBJECT

SESSION	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
1	-	N	-	N	N	N	Y	N	N	N
2	-	N	-	N	N	N	N	Y	N	N
3	-	N	-	N	Y	Y	Y	Y	N	N
4	N	N	-	N	Y	Y	N	Y	N	N
5	N	Y	-	N	N	N	N	Y	N	N
6	N	N	-	N	Y	Y	N	Y	N	N

90 DAY OLD (con't).

SESSION	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
1	-	-	N	-	N	N	N	N	N	N
2	-	-	Y	-	N	N	N	N	N	N
3	-	-	Y	-	N	N	N	N	Y	N
4	-	-	N	-	N	Y	N	N	N	N
5	N	-	N	-	N	N	N	N	Y	N
6	-	N	Y	-	N	N	-	N	Y	N

Table 9. Weaning weight (WW), capture weight (CW) and litter size for subjects in Experiment 1 (Chapter 5); The Influence of Age and Experience. Weights are expressed in grams.

30 DAY OLD

SUBJECT

	M 1	M 2	M 3	M 4	M 6	M 7	M 8	M 9	M 10	M 11	M 13	M 14
WW	29	27	21	24	31	23	25	32	24	33	24	22
CW	47	50	39	40	55	29	35	70	51	52	34	38
LS	7	7	5	12	7	5	3	6	8	13	13	7

30 DAY OLD (con't).

	F 1	F 2	F 3	F 4	F 7	F 8	F 9	F 10	F 11	F 12	F 13
WW	28	24	26	27	31	29	25	23	36	31	26
CW	49	47	51	36	59	58	61	54	52	49	31
LS	5	12	7	7	6	9	9	9	13	9	13

40 DAY OLD

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 12	M 13	M 14
WW	26	49	24	52	43	23	26	36	32	35	24	32	25
CW	58	82	58	72	75	48	55	83	55	55	44	67	40
LS	5	7	5	4	4	5	5	6	6	8	13	9	13

40 DAY OLD (con't).

	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 10	F 11	F 12	F 13	F 14
WW	34	28	22	22	24	26	29	30	29	32	30	26	27
CW	82	61	48	51	55	48	61	67	59	68	54	43	39
LS	7	7	5	12	12	12	8	3	6	13	9	13	7

Table 9, continued.

437.

50 DAY OLD

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11	M 12	M 13	M 14
WW	29	24	48	27	34	24	30	31	45	36	31	36	27	26
CW	59	61	91	74	49	53	81	93	68	66	60	55	62	64
IS	5	7	4	5	4	6	9	9	2	8	13	9	9	13

50 DAY OLD (con't).

	F 1	F 2	F 3	F 4	F 5	F 7	F 8	F 11	F 12	F 14
WW	28	26	29	25	29	36	30	21	31	29
CW	78	51	76	65	71	56	58	65	62	68
IS	5	12	12	7	7	8	6	13	9	7

90 DAY OLD

SUBJECT

	M 1	M 2	M 4	M 5	M 7	M 8	M 9	M 10	M 12	M 14
WW	30	24	24	41	41	23	29	27	30	25
CW	83	84	75	93	94	69	82	86	73	100
IS	7	12	7	4	4	2	9	6	13	13

90 DAY OLD (con't).

	F 2	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 14
WW	21	26	27	41	27	37	31	31	32	27
CW	84	78	70	90	108	96	76	80	89	85
IS	12	6	6	2	8	8	6	9	9	7

Table 10. Raw latency to capture in Experiment 2 (Chapter 6); The Emergence of the Behaviour. Latency scores are in minutes.

S	AGE TESTED	CAPTURE	LATENCY
M 1	21	Yes	90^c
M 2	23	No	-
M 3	24	No	-
M 4[b]	27	-	-
M 5	27	Yes	90^c
M 6	20	Yes	4.2
M 7	26	Yes	240^c
M 8	28	Yes	80^c
M 9	29	Yes	10.7
M 10	22	Yes	480^c
M 11	23	Yes	10
M 12	20	Yes	480^c
M 13	22	Yes	480^c
M 14[b]	26	-	-
M 15	25	No	-
M 16	26	Yes	63
M 17	27	Yes	5.5
M 18	23	Yes	120^c
M 19	26	Yes	20^c
M 20[b]	21	-	-
M 21	28	Yes	20^c
M 22	24	No	-
M 23	25	Yes	50^c
M 24[b]	29	-	-
M 25[b]	23	-	-

Table 10, continued.

S	AGE TESTED	CAPTURE	LATENCY
F 1	22	No	-
F 2[b]	29	-	-
F 3	26	Yes	40[c]
F 4	22	Yes	3.1
F 5	23	Yes	5.7
F 6	24	Yes	10
F 7[b]	28	-	-
F 8	25	Yes	30[c]
F 9	27	Yes	60[c]
F 10	23	Yes	60[c]
F 11	22	Yes	9.9
F 12[b]	20	-	-
F 13	24	Yes	60[c]
F 14	25	Yes	10
F 15	24	Yes	480[c]
F 16	29	Yes	5.5
F 17	20	No	-
F 18	25	Yes	5.3
F 19	29	Yes	10
F 20	26	Yes	.59
F 21	21	Yes	120[c]
F 22	27	Yes	14.8
F 23[b]	20	-	-

[b] Dead prior to test

[c] Approximate latency

Table 11. Raw latency to capture in Experiment 3 (Chapter 7); The Frequency of Prey Presentation. Latency scores are in seconds.

GROUP I: ITI-1

SUBJECT

SESSION	M 2	M 4	M 5	M 6	M 7	F 1	F 2	F 3	F 5	F 6
1	300	29	300	300	300	94	300	43	300	300
2	80	36	300	145	300	10	300	28	300	300
3	77	22	300	55	300	13	300	13	300	300
4	105	31	300	33	300	8	300	9	300	300
Retest	20	15	24	16	26	86	70	24	60	24

GROUP II: ITI-5

SUBJECT

SESSION	M 1	M 2	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 7	F 8
1	300	300	300	300	300	300	75	300	300	300	58
2	300	300	300	300	300	300	32	300	185	300	34
3	300	300	300	38	33	106	29	300	137	299	25
4	40	300	300	30	18	33	54	300	41	300	24
Retest	30	90	66	20	29	50	30	63	20	20	20

GROUP III: ITI-10

SUBJECT

SESSION	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4	F 5	F 6	F 7
1	103	300	179	300	300	81	300	300	300	63	300	300
2	91	300	29	47	300	76	300	300	300	43	300	56
3	41	300	35	32	300	30	300	44	276	36	300	36
4	25	300	66	25	300	13	300	49	300	29	300	41
Retest	22	42	20	20	**	36	25	18	28	20	30	20

** Dead prior to retest

Table 12. Raw latency to capture in Experiment 4a (Chapter 8); The Nature of the Experience. Latency scores are in seconds.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 10
1	300	47	25	300	300	111	300	89	300
2	300	36	33	300	272	54	32	33	300
3	300	51	40	300	58	33	59	10	99
4	300	33	8	300	300	24	29	19	102
5	300	25	19	300	199	39	40	17	300
6	300	23	24	300	232	34	25	10	107

PRE-CAPTURE (con't).

SESSION	F 1	F 2	F 3	F 5	F 6	F 7
1	300	210	26	25	27	41
2	300	300	27	38	40	300
3	300	293	25	40	93	55
4	97	91	30	44	25	40
5	300	44	115	51	105	89
6	37	69	53	39	40	29

POST-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	112	67	300	300	59	281	300	52	40
2	37	96	156	300	49	59	300	57	51
3	25	66	42	117	75	24	300	300	40
4	31	68	47	94	37	33	300	202	44
5	39	37	34	132	118	30	300	77	29
6	44	50	26	216	20	35	300	300	25

Table 12, continued.

POST-CAPTURE (con't).

SESSION	F 1	F 3	F 4	F 5	F 6	F 7	F 10
1	71	67	46	37	7	34	299
2	72	59	35	36	76	61	36
3	43	83	35	22	35	29	300
4	47	35	21	24	29	30	97
5	38	44	49	61	44	49	300
6	49	35	36	10	39	46	66

CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	10	53	149	57	47	8	300	295	8
2	11	47	35	27	32	10	300	30	21
3	127	53	71	63	300	22	300	58	10
4	25	87	300	49	101	24	71	53	13
5	24	120	32	39	67	7	299	52	6
6	129	33	300	40	33	5	300	29	17

Table 12, continued.

CAPTURE (con't).

	F 1	F 2	F 3	F 4	F5	F 6	F8
1	29	34	32	79	45	25	43
2	62	24	33	41	7	32	33
3	31	33	25	52	10	30	28
4	108	18	25	27	10	57	299
5	156	8	24	28	17	21	20
6	35	25	26	24	6	88	224

SESSION

Table 13. Raw frequency of exploration in Experiment 4a (Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 10
1	2	3	1	4	3	8	6	4	7
2	2	1	3	3	2	3	2	1	12
3	2	1	1	6	3	7	2	1	5
4	1	4	1	2	6	2	2	1	4
5	2	1	3	2	13	4	2	1	8
6	2	3	3	5	5	1	1	1	8

PRE-CAPTURE (con't).

SESSION	F 1	F 2	F 3	F 5	F 6	F 7
1	16	10	1	1	1	5
2	4	10	1	4	3	17
3	7	4	1	4	1	3
4	4	4	1	2	1	3
5	9	3	7	4	2	10
6	2	5	4	1	5	2

POST-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 9	M 10
1	10	14	5	7	6	16	17	7	5
2	7	8	4	7	3	1	7	4	3
3	1	6	3	4	5	1	2	6	4
4	5	6	1	4	4	2	3	9	1
5	1	3	2	6	7	2	6	4	3
6	5	6	3	2	8	3	7	8	2

Table 13, continued.

POST—CAPTURE (con't).

SESSION	F 1	F 3	F 4	F 5	F 6	F 7	F 10
1	8	4	3	1	1	2	28
2	4	5	2	3	7	5	5
3	7	3	1	1	1	1	21
4	3	3	1	1	2	1	11
5	3	7	5	2	1	3	30
6	3	2	1	1	4	1	6

CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	1	2	9	6	2	1	1	16	1
2	1	5	1	2	3	2	0	3	1
3	11	5	1	8	2	2	2	2	1
4	1	-6	6	4	4	1	5	9	1
5	1	10	3	3	3	1	11	2	1
6	10	3	3	1	3	1	3	1	1

CAPTURE (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 8
1	2	2	2	3	5	3	3
2	4	1	1	4	1	2	2
3	2	1	1	3	2	2	1
4	1	2	2	2	2	6	11
5	4	1	1	2	2	2	1
6	2	1	3	1	1	3	4

Table 14. RAW FREQUENCY OF WITHDRAWAL IN EXPERIMENT 4a (CHAPTER 8); THE NATURE OF THE EXPERIENCE.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 10
1	0	0	0	2	1	0	0	0	0
2	1	0	0	1	0	0	0	0	1
3	0	2	0	4	0	0	0	0	0
4	0	1	0	1	1	0	0	0	1
5	0	0	0	1	0	0	0	0	0
6	0	0	0	2	1	0	0	0	0

PRE-CAPTURE (CON'T).

SESSION	F 1	F 2	F 3	F 5	F 6	F 7
1	10	0	0	0	0	1
2	0	2	0	0	0	11
3	4	0	0	1	0	0
4	0	2	0	0	0	0
5	5	2	0	0	0	4
6	1	0	0	0	0	0

POST-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 9	M10
1	3	3	5	2	0	4	1	1	0
2	1	0	0	0	1	0	2	1	0
3	0	0	1	0	1	0	0	2	0
4	0	3	0	0	0	0	0	2	0
5	0	1	0	0	0	0	0	1	0
6	1	0	0	0	0	0	1	3	0

Table 14, CONTINUED.

POST - CAPTURE (CON'T).

SESSION	F 1	F 3	F 4	F 5	F 6	F 7	F 10
1	0	F2	0	0	0	0	16
2	0	1	0	0	1	2	0
3	0	1	0	0	0	0	10
4	0	0	0	0	0	0	2
5	0	0	0	0	0	0	17
6	0	0	0	0	0	0	2

CAPTURE
SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	0	0	2	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	0	0	2	0	2	0	1	0	0
4	0	0	0	0	0	0	0	1.	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	2	0	0

CAPTURE (CON'T).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 8
1	0	0	0	1	1	0	0
2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0
4	0	0	0	0	0	0	1
5	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0

Table 15. Raw frequency of nip in Experiment 4a (Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 10
SESSION	1	0	3	1	0	0	10	7	2	1
	2	0	1	3	0	3	6	3	1	7
	3	0	1	5	0	4	2	5	1	6
	4	0	2	1	0	0	1	1	1	6
	5	0	1	1	0	1	4	1	1	1
	6	0	2	2	4	4	2	1	1	5

PRE-CAPTURE (con't).

		F 1	F 2	F 3	F 5	F 6	F 7
SESSION	1	0	7	1	1	2	5
	2	2	2	1	2	2	4
	3	0	1	1	1	1	4
	4	4	3	1	2	1	3
	5	0	3	3	2	2.	3
	6	2	3	3	1	2	2

POST-CAPTURE

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 9	M 10
SESSION	1	4	5	0	5	6	10	0	6	4
	2	3	4	3	4	3	1	0	4	2
	3	1	3	3	4	3	1	0	0	3
	4	2	5	1	5	1	2	0	2	1
	5	2	2	2	3	5	2	0	3	2
	6	3	4	3	7	3	1	0	0	2

Table 15, continued.

POST-CAPTURE (con't).

	F 1	F 3	F 4	F 5	F 6	F 7	F 10
1	3	3	2	1	1	2	17
2	3	6	2	1	6	5	7
3	5	4	1	1	1	1	3
4	1	4	1	1	2	1	8
5	1	4	6	2	1	1	9
6	3	2	3	1	4	1	5

SESSION (row label, left side)

CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	1	3	11	3	2	1	0	5	1
2	1	4	1	2	2	2	0	3	1
3	7	3	2	4	0	2	0	1	1
4	1	1	1	4	4	1	3	2	1
5	2	4	2	1	2	1	1	3	1
6	5	2	0	3	1	1	0	1	1

SESSION (row label, left side)

CAPTURE (con't).

	F 1	F 2	F 3	F 4	F 5	F 6	F 8
1	1	2	1	3	3	2	2
2	2	1	1	2	1	2	2
3	2	1	1	3	1	2	1
4	4	1	1	1	1	2	7
5	2	1	1	1	1	1	1
6	2	1	1	1	1	1	4

SESSION (row label, left side)

Table 16. Raw frequency of unsuccessful capture in Experiment 4a (Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 10
1	0	2	0	0	0	3	6	0	0
2	0	0	2	0	1	4	2	0	2
3	0	1	2	0	2	0	4	0	1
4	0	0	0	0	0	0	0	0	2
5	0	0	0	0	0	0	0	0	0
6	0	0	0	2	2	1	0	0	1

PRE-CAPTURE (con't).

SESSION	F 1	F 2	F 3	F 5	F 6	F 7
1	0	1	0	0	1	2
2	1	0	0	0	0	0
3	0	0	0	0	0	1
4	4	0	0	1	0	1
5	0	1	1	1	0	2
6	1	0	2	0	1	0

POST-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 9	M 10
1	0	2	0	1	2	3	0	3	0
2	0	1	2	2	0	0	0	1	1
3	1	5	2	2	0	0	0	0	1
4	1	3	3	4	0	0	0	0	0
5	1	2	2	3	3	0	0	0	0
6	1	2	1	5	2	0	0	0	0

Table 16, continued.

POST-CAPTURE (con't).

SESSION	F 1	F 3	F 4	F 5	F 6	F 7	F 10
1	0	0	1	0	0	1	5
2	3	2	1	1	3	0	3
3	0	1	1	0	0	0	0
4	2	0	0	0	0	0	5
5	0	0	3	1	0	1	0
6	0	0	0	0	1	2	2

CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9
1	0	2	0	0	1	0	0	2	0
2	0	1	1	0	1	0	0	2	0
3	3	1	1	1	0	0.	0	0	0
4	0	1	0	1	3	0	2	0	0
5	1	1	0	0	1	0	0	2	0
6	3	0	0	3	0	0	0	0	0

CAPTURE (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 8
1	0	1	1	0	0	0	0
2	1	0	0	1	0	0	1
3	1	0	0	2	0	1	0
4	5	0	0	0	0	1	3
5	3	0	0	0	0	0	0
6	1	0	0	0	0	0	3

Table 17. Raw latency to capture in Experiment 4b (Chapter 8); The Nature of the Experience. Latency scores are in seconds.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	28	68	300	300	27	300	97	300	25	300	44
2	27	300	300	300	21	213	76	300	102	300	28
3	21	198	300	103	23	65	87	300	63	300	35
4	22	44	300	69	71	70	91	300	38	300	25
5	24	16	300	300	33	300	197	300	28	300	29
6	11	13	300	56	28	89	90	150	19	117	25

POST-CAPTURE

SUBJECT

SESSION	M 2	M 3	M 4	M 6	F 1	F 2	F 3	F 4	F 5
1	67	45	29	300	300	63	60	13	300
2	44	51	37	300	300	51	51	11	300
3	27	24	65	300	300	292	292	18	300
4	44	24	25	300	40	74	74	25	261
5	34	43	29	300	31	61	61	33	300
6	25	40	28	71	89	50	50	27	300

CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	13	22	59	300	32	31	25	300	37	25	38
2	24	30	300	300	190	20	93	38	14	23	28
3	7	44	300	300	234	12	60	48	20	27	20
4	16	36	300	300	95	21	31	17	22	20	21
5	8	34	119	300	168	20	29	50	16	20	37
6	10	29	300	300	53	17	69	21	18	36	42

Table 17, continued.

PRE-POST

SUBJECT

SESSION	M 1	M 2	M 4	M 5	M 6	F 1	F 2	F 4	F 6
1	200	33	21	17	28	44	29	56	28
2	300	21	33	14	41	31	32	300	21
3	36	21	39	29	49	28	46	152	30
4	22	40	42	18	51	300	300	115	17
5	27	47	33	17	30	135	245	167	19
6	34	21	66	21	30	17	29	299	36

CONTROL

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5	F 6
1	82	42	300	300	300	300	69	300	163	65	300
2	43	32	300	300	300	300	32	300	33	22	300
3	17	109	300	300	300	300	44	90	33	67	300
4	35	22	300	300	300	300	14	54	47	22	300
5	51	21	300	300	300	300	22	34	30	94	300
6	30	47	300	300	300	300	15	42	21	26	300

Table 18. Raw frequency of exploration in Experiment 4b (Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	2	5	8	13	1	21	6	12	1	4	2
2	2	21	8	9	1	11	7	6	1	8	2
3	1	16	18	11	1	8	5	4	4	3	5
4	1	5	10	12	6	2	7	6	4	4	3
5	3	3	5	16	5	10	22	4	1	4	4
6	1	2	3	5	1	6	6	16	1	11	3

POST-CAPTURE

SUBJECT

SESSION	M 2	M 3	M 4	M 6	F 1	F 2	F 3	F 4	F 5
1	8	2	4	16	17	8	7	3	13
2	4	5	7	10	12	5	4	1	9
3	2	1	9	4	10	17	5	1	8
4	2	2	2	6	5	4	1	1	31
5	2	3	2	6	5	3	4	1	8
6	1	4	3	8	1	5	5	1	7

CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	1	1	2	9	3	1	1	2	5	1	1
2	2	2	11	1	15	1	3	4	2	1	3
3	2	4	3	5	16	1	6	4	2	2	2
4	1	3	4	1	9	1	1	1	2	1	2
5	1	3	6	2	13	2	1	2	2	1	6
6	2	3	11	2	5	1	5	1	1	2	4

Table 18, continued.

PRE & POST CAPTURE

SUBJECT

SESSION	M 1	M 2	M 4	M 5	M 6	F 1	F 2	F 4	F 6
1	9	4	3	1	3	5	2	3	2
2	18	1	4	1	8	2	3	15	1
3	4	1	7	4	4	3	4	9	3
4	2	3	3	1	7	8	7	11	1
5	3	8	5	1	2	8	5	9	2
6	3	1	6	1	2	1	1	15	6

CONTROL

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5	F 6
1	7	1	10	9	18	11	5	15	6	3	6
2	4	2	6	4	5	2	3	12	2	1	5
3	1	1	5	8	6	2	3	8	1	3	3
4	2	2	1	23	1	1	1	6	1	2	1
5	3	3	5	1	7	6	2	2	1	3	5
6	2	2	4	5	7	3	2	9	1	2	8

Table 19. Raw frequency of withdrawal in Experiment 4b
(Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	0	1	1	8	0	2	0	5	0	1	0
2	0	0	0	0	0	1	0	2	0	5	0
3	0	0	0	4	0	1	0	2	0	1	0
4	0	1	0	1	0	0	2	0	0	1	0
5	0	1	0	2	0	1	8	1	0	2	1
6	0	0	0	2	0	0	1	4	0	5	0

SESSION

POST-CAPTURE

SUBJECT

	M 2	M 3	M 4	M 6	F 1	F 2	F 3	F 4	F 5
1	0	0	1	2	3	0	2	0	3
2	0	0	1	1	2	0	0	0	4
3	0	0	3	0	3	3	1	0	2
4	0	0	0	0	0	0	0	0	12
5	0	0	0	0	0	0	1	0	0
6	0	2	0	0	0	0	0	0	2

SESSION

CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	0	0	1	1	0	0	0	1	3	0	0
2	0	0	9	1	5	0	0	1	0	0	0
3	0	0	2	1	9	0	1	1	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	2	0	3	0	0	0	1	0	0
6	0	0	1	0	1	0	0	0	0	0	0

SESSION

Table 19, continued.

PRE & POST CAPTURE

SUBJECT

SESSION	M 1	M 2	M 4	M 5	M 6	F 1	F 2	F 4	F 6
1	0	0	0	0	0	1	0	0	0
2	1	0	0	0	0	0	0	4	0
3	0	0	2	0	0	0	3	1	0
4	0	0	0	0	0	2	0	0	0
5	0	2	0	0	0	0	0	0	0
6	0	0	1	0	0	0	0	1	0

CONTROL

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5	F 6
1	0	0	3	4	8	1	0	7	0	0	6
2	0	0	2	2	2	1	0	1	0	0	1
3	0	0	1	2	1	0	0	1	0	0	1
4	0	0	1	2	1	0	0	0	0	0	1
5	0	0	1	0	3	2	0	0	0	0	2
6	0	0	1	3	4	1	0	1	0	0	5

Table 20. Raw frequency of nip in Experiment 4b
(Chapter 8); The Nature of the Experience.

PRE-CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	2	4	4	0	1	0	7	1	1	0	2
2	1	0	6	4	1	5	7	0	4	0	1
3	1	6	11	6	1	3	8	0	4	0	5
4	2	4	2	2	5	2	9	0	3	0	2
5	3	2	0	2	2	0	14	0	1	0	2
6	1	1	1	2	1	4	8	6	1	6	2

(SESSION)

POST-CAPTURE

SUBJECT

	M 2	M 3	M 4	M 6	F 1	F 2	F 3	F 4	F 5
1	3	1	4	0	1	6	5	1	8
2	3	2	4	0	3	5	2	1	0
3	1	1	5	0	4	11	1	1	8
4	1	2	1	0	4	5	1	1	17
5	3	2	1	0	4	2	2	1	5
6	1	1	3	5	1	5	1	1	1

(SESSION)

Table 20, continued.

CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	1	1	3	1	4	3	1	0	1	2	1
2	2	2	0	0	10	1	3	3	2	3	2
3	1	1	0	0	8	1	4	2	1	2	1
4	1	3	0	0	7	1	2	1	2	1	1
5	1	2	5	0	9	1	1	2	3	1	4
6	2	2	0	0	4	1	4	1	2	3	3

(SESSION down the left side)

PRE & POST CAPTURE

SUBJECT

	M 1	M 2	M 4	M 5	M 6	F 1	F 2	F 4	F 6
1	6	2	1	1	2	3	2	6	1
2	3	1	2	1	2	2	2	8	1
3	3	1	3	2	2	2	2	7	1
4	2	1	2	1	2	0	0	9	1
5	3	3	2	1	2	3	2	4	2
6	2	1	1	1	1	1	1	10	2

(SESSION down the left side)

CONTROL

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5	F 6
1	7	1	0	0	0	0	2	3	3	3	0
2	3	1	0	0	0	0	1	0	2	1	0
3	1	1	0	0	0	0	2	3	1	3	0
4	2	2	0	0	0	0	1	10	1	2	0
5	1	1	0	0	0	0	1	4	1	5	0
6	2	1	0	0	0	0	1	6	2	2	0

(SESSION down the left side)

Table 21. Raw frequency of unsuccessful capture in Experiment 4b (Chapter 8); The Nature of the Experience.

PRE—CAPTURE

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	1	1	0	0	0	0	6	0	0	0	1
2	0	0	0	1	0	4	6	0	3	0	0
3	0	1	5	4	0	2	6	0	1	0	2
4	1	0	0	0	4	1	4	0	2	0	0
5	1	1	0	0	1	0	2	0	0	0	1
6	0	0	0	1	0	1	5	0	0	1	0

POST—CAPTURE

SUBJECT

SESSION	M 2	M 3	M 4	M 6	F 1	F 2	F 3	F 4	F 5
1	2	0	0	0	0	3	3	0	4
2	1	1	2	0	0	2	2	0	0
3	0	0	1	0	8	7	0	0	4
4	0	0	0	0	0	6	0	0	3
5	1	0	0	0	0	3	1	0	4
6	0	0	1	3	0	3	0	0	1

Table 21, continued.

CAPTURE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
1	0	0	2	0	0	2	0	0	0	1	0
2	1	1	0	0	2	0	1	2	0	1	0
3	0	0	0	0	3	0	3	1	0	1	0
4	0	2	0	0	4	0	1	0	1	0	0
5	0	1	2	0	6	0	1	1	0	0	3
6	0	1	0	0	1	0	3	0	1	1	2

(SESSION — rows 1–6)

PRE & POST CAPTURE

SUBJECT

	M 1	M 2	M 4	M 5	M 6	F 1	F 2	F 4	F 6
1	4	0	0	0	0	2	0	5	1
2	0	0	0	0	1	0	0	0	0
3	0	0	1	0	1	0	0	6	1
4	1	0	0	0	0	0	0	3	0
5	2	1	0	0	0	1	1	2	1
6	1	0	0	0	0	0	0	7	1

(SESSION — rows 1–6)

CONTROL

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5	F 6
1	5	1	0	0	0	0	0	0	0	0	0
2	2	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	1	0	0	0
4	1	1	0	0	0	0	0	3	0	1	0
5	0	0	0	0	0	0	0	1	1	0	0
6	1	0	0	0	0	0	0	0	0	1	0

(SESSION — rows 1–6)

Table 22. Incidence of capture in Experiment 4c
(Chapter 8); The Nature of the Experience.
Y indicates capture; N indicates no capture.

CAPTOR-EAT

SESSION

SUBJECT	1	2	3	4	5	6	7	8	9	10	11	12
F 1	Y	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
M 20	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 20	Y	Y	Y	Y	Y	Y	Y	N	Y	N	Y	Y

CAPTOR-NO EAT

SESSION

SUBJECT	1	2	3	4	5	6	7	8	9	10	11	12
F 2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 6	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
M 15	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
M 19	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y

Table 22, continued.

NON CAPTOR-NO EAT

SESSION

	1	2	3	4	5	6	7	8	9	10	11	12
F 1	N	Y	Y	Y	N	N	N	N	N	N	N	N
F 3	Y	Y	Y	Y	N	N	N	N	N	N	N	N
F 12	N	N	N	N	N	N	N	N	N	N	N	N

SUBJECT

NON CAPTOR-EAT

SESSION

	1	2	3	4	5	6	7	8	9	10	11	12
M 1	Y	Y	Y	Y	Y	N	N	Y	Y	Y	N	N
M 10	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
F 11	N	N	N	Y	N	N	N	N	Y	N	N	N

SUBJECT

Table 23. Raw latency to capture in Experiment 5a (Chapter 9); The Effect of Early Dead Eat. Latency scores are in seconds.

GROUP I

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7
1	300	85	300	300	300	300	300
2	295	20	300	300	300	300	300
3	33	40	300	31	300	300	300

GROUP I (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 9	F 10
1	300	300	300	300	300	300	300	300	300	180
2	300	300	300	300	300	300	300	300	300	55
3	300	300	300	300	300	300	300	26	300	300

GROUP II

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 7	M 8	M 9
1	300	300	300	300	300	300	300
2	300	300	300	300	300	300	300
3	300	300	300	300	300	300	300

Table 23, continued.

GROUP II (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7[a]
1	300	300	45	300	250	300	300
2	300	300	90	300	26	300	—
3	300	300	70	300	44	300	—

CONTROL

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	M 7	M 8	M 9	M 10	M 11
1	300	300	300	300	300	295	300	300	300	300	126
2	300	300	300	300	300	260	90	300	300	300	70
3	300	300	300	300	300	41	45	200	300	300	25

CONTROL (con't).

SESSION	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12
1	300	300	300	300	300	300	46	300	83	105	300	300
2	300	300	300	300	300	300	40	300	24	75	300	200
3	300	300	75	300	300	300	55	300	80	45	300	22

[a] Subject F 7 was not included in the statistical analysis.

Table 24. Raw latency to capture in Experiment 5b (Chapter 9); The Influence of Age and Treatment - Test Interval. Latency scores are in seconds.

EARLY EAT - EARLY TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4	F 5
1	53	80	70	255	22	300	55	62	60	32	300
2	–	–	–	–	–	300	–	–	–	–	300
3	–	–	–	–	–	300	–	–	–	–	300

EARLY EAT - LATE TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4	F 5
1	300	63	49	189	52	300	56	20	34	48	300
2	300	–	–	–	–	300	–	–	–	–	300
3	300	–	–	–	–	300	–	–	–	–	300

NO EAT - EARLY TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4	F 5
1	300	300	300	35	300	300	97	300	40	66	300
2	300	300	300	–	300	300	–	300	–	–	300
3	300	300	300	–	300	300	–	300	–	–	300

Table 24, continued.

LATE EAT — LATE TEST

SUBJECT

		M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
SESSION	1	180	80	122	300	38	300	183	69	95	42	300
	2	—	—	—	300	—	300	—	—	—	—	300
	3	—	—	—	300	—	300	—	—	—	—	300

NO EAT — LATE TEST

SUBJECT

		M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5	F 6
SESSION	1	37	300	61	34	300	300	300	300	·67	300	300
	2	—	300	—	—	300	300	300	300	—	300	300
	3	—	300	—	—	300	300	300	300	—	300	300

Table 25. Raw latency to capture in Experiment 5c (Chapter 9); Dissociation of the Post-Capture Experience. Latency scores are in seconds.

CUBED LOCUST

SUBJECT

		M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5
SESSION	1	36	300	300	300	300	193	139	160	300	300
	2	19	300	300	300	300	300	39	53	300	86
	3	29	300	300	300	300	300	41	32	˙53	28
	4	6	300	300	300	300	300	21	47	48	17

EVISCERATED

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4
SESSION	1	103	300	31	137	166	300	21	37	75	300
	2	109	300	49	90	87	300	21	18	20	300
	3	71	300	28	35	79	300	17	29	55	300
	4	32	300	26	20	20	300	15	34	44	300

Table 25, continued.

DEAD WHOLE LOCUST

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 3	F 4
1	76	99	27	88	166	300	30	40	35	300
2	39	13	35	300	78	242	21	77	300	300
3	36	51	17	300	300	46	15	27	300	300
4	27	11	24	56	43	28	65	48	29	96

SESSION

CONTROL

SUBJECT

	M 1	M 2	M 3	M 4	M 5	F 1	F 2	F 3	F 4	F 5
1	300	56	79	300	300	300	67	48	300	72
2	41	13	26	112	300	300	32	39	300	63
3	41	17	71	41	300	300	49	26	300	26
4	32	22	63	25	300	300	25	24	300	25

SESSION

Table 26. Raw latency to capture in Experiment 6a
(Chapter 10); Sensory Pre-exposure: The Relative
Importance of Olfaction and Vision. Latency scores
are in seconds.

PERFORATED CUBE

SUBJECT

		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
SESSION	1	49	25	143	23	41	300	300	300
	2	34	17	278	26	44	52	300	300

PERFORATED CUBE (con't).

		M 1	M 2	M 3	M 4	M 5	M 6	M 7
SESSION	1	300	47	300	300	300	300	132
	2	57	40	300	300	300	300	86

SOLID CUBE

SUBJECT

		F 1	F 2	F 3	F 4	F 6	F 7
SESSION	1	186	78	300	90	86	300
	2	39	41	300	51	25	300

Table 26, continued.

SOLID CUBE (con't).

SESSION		M 1	M 2	M 3	M 4	M 5
	1	59	95	43	300	89
	2	21	17	17	300	17

EMPTY CUBE

SUBJECT

SESSION		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
	1	48	32	181	148	77	55	75	21
	2	35	41	300	62	184	36	34	28

EMPTY CUBE (con't).

SESSION		M 1	M 2	M 3	M 4	M 5	M 6
	1	47	300	300	35	300	300
	2	31	300	300	47	300	300

Table 27. Raw frequency of exploration in Experiment 6a (Chapter 10); Sensory Pre-exposure: The Relative Importance of Olfaction and Vision.

PERFORATED CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5
SESSION	1	6	3	2	4	4
	2	1	1	1	7	1

PERFORATED CUBE (con't).

		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
SESSION	1	5	4	20	14	6	6	5	1
	2	2	2	7	2	3	3	1	2

SOLID CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6
SESSION	1	6	12	7	1	12	12
	2	1	4	2	6	1	4

Table 27, continued.

SOLID CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
	1	10	2	10	1	4	9	13	7
	2	2	1	14	1	1	8	14	7

EMPTY CUBE

SUBJECT

SESSION		M 1	M 2	M 3	M 4	M 5	M 6	M 7
	1	9	7	16	7	16	19	9
	2	5	1	3	8	3	10	5

EMPTY CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 6	F 7
	1	17	6	20	2	14	21
	2	4	1	2	8	1	4

Table 28. Raw frequency of withdrawal in Experiment 6a
(Chapter 10); Sensory Pre-exposure: The Relative
Importance of Olfaction and Vision.

PERFORATED CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5
SESSION	1	2	0	0	1	0
	2	0	0	0	4	0

PERFORATED CUBE (con't).

		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
SESSION	1	0	0	1	2	0	0	2	0
	2	0	0	2	1	0	0	0	0

SOLID CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6
SESSION	1	0	4	1	0	5	8
	2	0	0	1	2	0	3

Table 28, continued.

Solid Cube (con't).

	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
SESSION 1	0	0	7	0	0	5	5	5
SESSION 2	0	0	0	0	0	1	8	2

EMPTY CUBE

SUBJECT

	M 1	M 2	M 3	M 4	M 5	M 6	M 7
SESSION 1	2	0	9	5	7	7	0
SESSION 2	0	0	2	1	2	2	0

EMPTY CUBE (con't).

	F 1	F 2	F 3	F 4	F 6	F 7
SESSION 1	7	0	2	2	10	10
SESSION 2	1	0	1	0	0	2

Table 29. Raw frequency of nip in Experiment 6a
(Chapter 10); Sensory Pre-exposure: The Relative
Influence of Olfaction and Vision.

PERFORATED CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5
SESSION	1	6	3	2	0	3
	2	1	1	1	1	1

Perforated Cube (con't).

		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
SESSION	1	5	4	11	8	3	5	8	1
	2	2	2	1	1	3	3	1	2

SOLID CUBE

SUBJECT

		M 1	M 2	M 3	M 4	M 5	M 6
SESSION	1	3	0	0	1	1	1
	2	1	0	0	3	0	0

Table 29, continued.

SOLID CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
	1	5	2	6	1	4	4	0	0
	2	2	1	7	1	1	6	0	0

EMPTY CUBE

SUBJECT

SESSION		M 1	M 2	M 3	M 4	M 5	M 6	M 7
	1	0	4	0	1	0	2	2
	2	3	1	0	3	0	1	1

EMPTY CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 6	F 7
	1	11	6	0	1	12	4
	2	3	1	0	5	1	0

Table 30. Raw frequency of unsuccessful capture
in Experiment 6a (Chapter 10); Sensory Pre-exposure:
The Relative Importance of Olfaction and Vision.

PERFORATED CUBE

SUBJECT

SESSION		M 1	M 2	M 3	M 4	M 5
	1	2	2	1	0	2
	2	0	0	0	0	0

PERFORATED CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
	1	2	1	1	0	2	3	2	0
	2	0	1	0	0	2	2	0	1

SOLID CUBE

SUBJECT

SESSION		M 1	M 2	M 3	M 4	M 5	M 6
	1	1	0	0	0	0	0
	2	0	0	0	1	0	0

Table 30, continued.

SOLID CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8
	1	3	0	1	0	1	2	0	0
	2	0	0	3	0	0	3	0	0

EMPTY CUBE

SUBJECT

SESSION		M 1	M 2	M 3	M 4	M 5	M 6	M 7
	1	0	1	0	0	0	0	0
	2	0	0	0	0	0	0	0

EMPTY CUBE (con't).

SESSION		F 1	F 2	F 3	F 4	F 6	F 7
	1	0	2	0	0	2	0
	2	0	0	0	3	0	0

Table 31. Raw latency to Capture in Experiment 6b (Chapter 10); Sensory Pre-exposure: The Influence of Age and Treatment - Test Interval. Latency scores are in seconds.

EARLY EXPOSURE – EARLY TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	F 1	F 2	F 3	F 4	F 5
1	300	300	300	300	62	23	300	300	300
2	300	300	300	300	*	*	300	300	300
3	300	300	300	300	*	*	300	300	300

EARLY EXPOSURE – LATE TEST

SUBJECT

SESSION	M 1	M 2	M 3	F 1	F 2	F 3	F 4
1	41	59	37	300	300	89	298
2	*	*	*	300	300	*	*
3	*	*	*	300	52	*	*

NO EXPOSURE – EARLY TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	F 1	F 2	F 3	F 4	F 5
1	300	300	240	300	300	210	300	60	300
2	300	300	*	300	300	*	300	*	300
3	300	300	*	300	300	*		*	53

* No test administered.

Table 31, continued.

LATE EXPOSURE – LATE TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	M 6	F 1	F 2	F 4	F 5
1	66	300	70	54	39	300	300	117	90	180
2	*	300	*	*	*	300	29	*	*	*
3	*	300	*	*	*	260	*	*	*	*

NO EXPOSURE – LATE TEST

SUBJECT

SESSION	M 1	M 2	M 3	M 4	M 5	F 1	F 4	F 5
1	54	300	300 -	47	300	300	300	300
2	*	300	158	*	220	300	57	61
3	*	300	*	*	*	300	*	*

Table **32.** Selective Breeding Experiments. Raw latency to capture for the strain of Non-Captors, generation one through eight. Latency scores are in seconds.

Generation of Pups: NC 1

Subject & Latency Score

Generation of ♀♀ : NC 0

♀♀ 1	M 1	M 2	M 3	F 1	F 3	F 4	F 5	F 6			
Latency	60	70	1800	70	60	186	40	80			
♀♀ 2	M 5	M 6	M 7	M 8	F 7	F 8	F 9	F 10	F 11	F 12	
Latency	105	90	667	1298	540	1800	1635	1535	195	1800	
♀♀ 3	M 9	M 10	M 12	M 13	M 14	M 15	M 16	F 13	F 14	F 15	F 16
Latency	20	537	100	48	1238	45	35	308	49	120	170
♀♀ 4	M 17	F 17									
Latency	380	67									
♀♀ 5	M 18	M 19	M 20	F 18	F19						
Latency	172	65	60	130	100						
♀♀ 6	M 21	M 22	F 20	F21	F22	F23					
Latency	430	1280	1800	685	1800	1800					

Generation of Pups: NC 2

Subject & Latency Score

Generation of ♀♀ : NC 1

♀♀ 1	M 1	M 2	F 1	F 3							
Latency	34	1530	1800	1800							
♀♀ 2	M 3	F 4	F 5	F 6							
Latency	1800	1800	1800	1800							
♀♀ 3	M 4	M 5	M 6	M 7	M 8	F 7	F 8	F 9	F 10	F 11	F 12
Latency	1600	60	1800	1730	1800	1800	90	1800	300	1800	230
♀♀ 4	M 9	M 10	M 11	F 13	F 14	F 15					
Latency	1800	1800	1800	1365	1800	1800					
♀♀ 5	M 12	M 13	M 14	F 16	F 17	F 18					
Latency	175	60	1800	1800	1800	1800					

Table **32**, continued.

Generation of Pups: NC 3

Subject & Latency Score

		M 1	M 2	M 3	M 4	F 1	F 2	F 3				
NC 2	♀♀ 1 Latency	1800	1245	1800	1170	1800	1800	1800				
	♀♀ 2 Latency	M 5 175	M 6 150	M 7 1800	M 8 35	F 4 1800	F 5 140	F 6 1800				
Generation of ♀♀:	♀♀ 3 Latency	M 9 1800	M 10 1312	M 11 1800	F 7 1800	F 8 110	F 9 710	F 10 360				
	♀♀ 4 Latency	M 12 1800	M 13 1800	M 14 660	M 15 240	F 11 1800	F 12 1800	F 13 1525				

Generation of Pups: NC 4

Subject & Latency Score

		M 1	M 2	F 1	F 2	F 3					
NC 3	♀♀ 1 Latency	60	60	1800	1800	60					
	♀♀ 2 Latency	M 3 63	M 4 1800	M 5 682	M 6 63	F 4 30	F 5 1800	F 6 120			
Generation of ♀♀:	♀♀ 3 Latency	M 7 1800	M 8 1800	M 9 100	M 10 1800	F 7 1800	F 8 160				
	♀♀ 4 Latency	M 11 110	M 12 150	M 13 1800	F 9 1800	F 10 136	F 11 145				
	♀♀ Latency	M 14 1800	M 15 40	F 12 1800	F 13 1800	F 14 1800	F 15 1140				
	♀♀ 6 Latency	M 16 1199	M 17 1800	M 18 1800	F 16 780	F 17 1290	F 18 45				

Table 32, continued.

Generation of Pups: NC 5

Subject & Latency Score

Generation of ♀♀ : NC 4

♀♀ 1	M 1	M 2	M 3	F 1	F 2	F 3					
Latency	1800	70	1800	93	160	1800					
♀♀ 2	M 4	M 5	M 6	F 4	F 5	F 6					
Latency	1800	1110	1800	1800	1800	1800					
♀♀ 3	M 7	M 8	M 9	F 7	F 8	F 9					
Latency	1245	50	260	70	63	50					
♀♀ 4	M 10	M 11	M 12	F 10	F 11	F 12					
Latency	177	109	1800	1800	118	40					
♀♀ 5	M 15	F 13	F 14	F 15							
Latency	545	206	1800	105							
♀♀ 6	M 16	M 17	M 18	M 19	F 16	F 17					
Latency	1800	445	1800	65	1800	1800					

Generation of Pups: NC 6

Subject & Latency Score

Generation of ♀♀ : NC 5

♀♀ 1	M 1	M 2	M 3								
Latency	1800	1800	1800								
♀♀ 2	M 5	M 6	M 7	M 8	F 1	F 2	F 3				
Latency	1800	1800	1800	1800	1800	1800	1800				
♀♀ 3	M 9	M 10	M 11	M 12	M 13	F 4	F 5	F 6	F 7		
Latency	1800	1800	1800	1800	1800	1800	1800	1800	1800		
♀♀ 4	M 14	M 15	M 16	M 17	M 18	M 19	M 20	F 8	F 9	F 10	
Latency	1800	1800	1800	1415	500	1800	837	1800	1800	820	
♀♀ 5	M 21	M 22	M 23	M24	M 25	M26	M 27	F 11	F 12	F 13	F 14
Latency	1800	180	1800	1800	1800	1301	840	1800	1800	1800	1800
♀♀ 6	F 15	F 16	F 17	F 18							
Latency	900	1800	1800	720							

Table **32**, continued.

Generation of Pups: NC 7

Subject & Latency Score

Generation of ♀♀: NC 6

♀♀ 1	M 1	M 2	F 1	F 2	F 3					
Latency	120	1800	177	360	120					
♀♀ 2	M 3	M 4	F 4	F 5						
Latency	1800	60	60	1800						
♀♀ 3	M 5	F 6	F 7	F 8	F 9					
Latency	1800	1800	1800	1800	240					
♀♀ 4	M 6	M 7	F 10							
Latency	1800	1800	1800							
♀♀ 5	M 8	M 9	M 10	F 11	F 12					
Latency	1800	130	1800	1800	1800					
♀♀ 6	M 11	M 12	M 13	F 13	F 14					
Latency	1800	1800	220	1800	63					
♀♀ 7	F 15	F 16								
Latency	1800	1800								
♀♀ 8	M 14	M 15	M 16	F 17						
Latency	1800	1800	1800	1800						
♀♀ 9	F 18	F 19								
Latency	1800	1800								

Generation of Pups: NC 8

Subject & Latency Score

Generation of ♀♀: NC 7

♀♀ 1	M 1	F 1	F 2							
Latency	390	120	1800							
♀♀ 2	M 2	M 3	F 3	F 4	F 5	F 6	F 7			
Latency	1800	1800	49	1800	1800	1800	1800			
♀♀ 3	M 4	M 5	F 8	F 9						
Latency	1800	1800	1800	1800						
♀♀ 4	M 6	M 9	M 10	F 10						
Latency	1800	1800	1387	1800						
♀♀ 5	M 11	M 12	M 13	F 11	F 12					
Latency	1800	1800	1800	840	810					
♀♀ 6	M 14	F 13	F 15	F 16						
Latency	1800	1800	1800	1800						

Table 33. Selective Breeding Experiments. Raw latency to capture for the strain of Captors, generation one through eight. Latency scores are in seconds.

Generation of Pups : C 1

Subject & Latency Score

♀♀ 1	M 1	M 2	M 3	M 4	F 1						
Latency	20	165	672	1800	265						
♀♀ 2	M 5	M 6	M 7	M 8	F 2	F 3	F 4	F 5			
Latency	1723	745	720	669	690	1800	740	50			
♀♀ 3	M 9	M 10	F 6	F 7	F 8						
Latency	45	36	110	1800	296						
♀♀ 4	M 11	M 12	M 13	M 14	M 16	F 9	F 10	F 11			
Latency	1800	662	90	120	1800	1800	1800	649			
♀♀ 5	M 17	M 18	M 19	F 12	F 13	F 14	F 15	F 16	F 17	F18	F 19
Latency	80	1374	330	840	1800	1800	630	70	1800	1800	1800

Generation of ♀♀ :: C 0 (left margin label)

Generation of Pups: C 2

Subject & Latency Score

♀♀ 1	M 1	M 2	M 3	M 4	F 1	F 2	F 3	F 4	F 5		
Latency	195	120	90	40	119	56	63	1800	1800		
♀♀ 2	M 5	M 6	M 7	M 8	M 9	M 10	F 6	F 7	F 8		
Latency	137	148	148	90	736	599	40	1288	330		
♀♀ 3	M 11	M 12	F 9	F 10	F 11	F 12	F 13	F 14			
Latency	38	25	111	50	148	1074	58	1800			
♀♀ 4	M 15	M 16	F 15	F 16	F 17	F 18					
Latency	77	43	150	162	40	208					
♀♀ 5	M 17	M 18	M 19	F 19	F 20						
Latency	1800	35	25	666	46						

Generation of ♀♀ :: C 1 (left margin label)

Table **33**, continued.

Generation of Pups: C 3

Generation of ♀♀ : C 2

Subject & Latency Score

♀♀ 1	M 1	M 2	M 3	F 1	F 2	F 3	F 4	F 5			
Latency	420	70	75	216	105	79	39	87			
♀♀ 2	M 4	M 5	M 6	F 6	F 7	F 8					
Latency	32	310	630	900	1800	780					
♀♀ 3	M 7	M 8	F 9	F 10							
Latency	60	94	60	92							
♀♀ 4	M 9	M 10	F 11	F 12	F 13	F 14	F 15	F 16			
Latency	1800	30	114	1800	64	1730	82	148			
♀♀ 5	F 17	F 18									
Latency	1800	158									

Generation of Pups: C 4

Generation of ♀♀ : C 3

Subject & Latency Score

♀♀ 1	M 1	M 2									
Latency	1800	30									
♀♀ 2	M 3	M 4	M 5	M 6	F 1	F 2					
Latency	1570	45	1245	140	40	1800					
♀♀ 3	M 7	M 8	M 9	F 3	F 4	F 5					
Latency	240	90	60	1800	1800	1800					
♀♀ 4	M 10	M 11	M 12	F 6	F 7	F 8					
Latency	80	1800	30	60	120	205					
♀♀ 5	M 13	M 14	F 9	F 10	F 11	F 12					
Latency	110	140	1220	28	62	1040					

Table **33**, continued.

Generation of Pups: C 5

Subject & Latency Score

♀♀ 1 Latency	M 1 828	M 2 32	F 1 120	F 2 50	F 3 740						
♀♀ 2 Latency	M 3 90	M 4 90	M 5 55	M 6 55	F 4 234	F 5 130	F 6 231				
♀♀ 3 Latency	M 7 1290	M 8 130	M 9 55	F 7 30	F 8 28	F 9 495					
♀♀ 4 Latency	M 10 599	M 11 49	M 12 48	F 10 60	F 11 74	F 12 45					
♀♀ 5 Latency	M 13 599	M 14 1320	M 15 55	F 13 635	F 14 1800	F 15 1800					
♀♀ 6 Latency	M 16 60	M 17 82	M 18 45	M 19 40	F 16 60	F 17 87					

Left margin: Generation of ♀♀ : C 4

Generation of Pups: 6

Subject & Latency Score

♀♀ 1 Latency	M 1 21	M 2 21	M 3 45	F 1 105	F 2 134	F 3 68					
♀♀ 2 Latency	M 4 47	M 5 92	M 6 35	F 4 31	F 5 27	F 6 40					
♀♀ 3 Latency	M 7 42	M 8 38	M 9 1800	F 7 1260	F 8 21	F 9 39					
♀♀ 4* Latency	M 10 75	M 11 52	F 10 312	F 11 1800	F 12 270	F 13 56	F 14 299				
♀♀ 5 Latency	M 12 70	M 13 100	M 14 841	F 15 271	F 16 40	F 17 1800					
♀♀ 6* Latency	M 15 52	M 16 126	M 17 143	M 18 60	F 18 105	F 19 62	F 20 87				

Left margin: Generation of ♀♀ : C 5

*Albino

489.

Table 33, continued.

Generation of Pups: C 7

Generation of ♀♀: C 6

Subject & Latency Score

♀♀ 1*	M 1	M 2	M 3	M 4	M5	F 1	F 2	F 3			
Latency	202	850	1800	148	1800	1800	990	1335			
♀♀ 2*	M 6	M 7	F 5	F 6	F 7						
Latency	1800	32	84	805	120						
♀♀ 3	M 8	M 9	M 10	M 11	M 12	F 8					
Latency	1240	60	170	90	250	1800					
♀♀ 4*	M 13	M 15	F 9	F 10	F 11						
Latency	200	210	35	86	127						
♀♀ 5	M 16	M 17	F 12								
Latency	73	60	180								
♀♀ 6	M 19	M 20	F 13	F 14	F 15	F 16	F 17				
Latency	30	1800	1260	330	20	30	33				

Generation of Pups: C 8

Generation of ♀♀: C 7

Subject & Latency Score

♀♀ 1*	M 1	F 1	F 2	F 3	F 4	F 5	F 6				
Latency	36	55	41	60	56	64	38				
♀♀ 2*	M 2	M 3	M 4	M 5	F 7	F 8	F 9	F 10			
Latency	1800	140	260	111	79	69	68	57			
♀♀ 3*	M 6	M 7	F 11	F 12	F 13	F 14					
Latency	690	72	1070	31	150	1800					
♀♀ 4*	M 8	M 9	M 10	M 11	F 15	F 16	F 17				
Latency	156	1056	675	53	1800	210	150				
♀♀ 5	M 12	M 13	F 18	F 19							
Latency	62	113	60	57							
♀♀ 6	M 14	M 15	M 16	M 17	M 18	M 19	F 20				
Latency	684	30	110	56	73	60	61				
♀♀ 7	M 20	M 21	M 22	M 23	F 21						
Latency	34	29	34	22	137						

* Albino

APPENDIX C

APPENDIX C

PUBLISHED PAPERS

The papers contained in this section were submitted for

publication and subsequently published at the time when this

treatise was in its final stages. The first paper, "Effects

of Novel Environment on Predatory Behaviour of Golden Hamsters",

consists of a small study which demonstrated that the independent

variable in question, that of a novel environment, could suppress

predation in the experienced locust captor. In the second paper,

a review, most of the material was taken from Chapter 2, Section

2.4b.6. However, the organization of the paper differs from the

way in which the material is laid out in the treatise and the

introduction is new; it is these two points the reader should

particularly note.

EFFECTS OF NOVEL ENVIRONMENT ON PREDATORY BEHAVIOR OF GOLDEN HAMSTERS[1]

RICHARD H. POLSKY

University of Leicester

Summary.—20 golden hamsters were tested for capture of locusts in several different cage conditions which included their own familiar home cage, a neutral cage, a hamster-soiled cage and a locust-soiled cage. *S*s showed a significantly greater latency to capture when taken from their own home cage and tested in a neutral cage, however, latencies decreased with repeated testing. Further, *S*s showed a relatively high latency to capture when tested in the locust-soiled cage. This later finding was explained in terms of prey camouflage.

One variable of basic importance which undoubtedly influences rodents' predatory behavior is that of a strange or unfamiliar environment. In most laboratory studies researchers have made an effort to control for this factor; rats, for example, have usually been tested in their own home cages or in a test cage to which they were allowed to acclimatize. The reasons for these precautions are clear; several investigators have found that a rat who was initially a highly reliable and consistent killer in its own home cage tended not to kill or kill with a great increase in latency after it had been put into a novel environment (Avis & Treadway, 1971; Baenninger & Ulm, 1969; DeSisto & Huston, 1970; Karli, 1956; Miley & Baenninger, 1972).

The well-known work of Karli (1956) illustrates this point most clearly. In one experiment he housed wild rats individually and then tested their reaction to mice immediately after being re-housed into new living quarters or after an interval of 2, 5, or 7 wk. Karli found a low incidence of killing by those rats who were tested immediately after being re-housed, however, the percentage of killers increased with the time spent in the housing enclosure; 30% did so after 2 wk., 60% after 5 wk. and 70% after 7 wk. In another experiment Karli took proven killers out of their own home cages and tested their reaction to mice in a novel circular pen. Again, he found that the killing latencies greatly increased when tested under these conditions; in some cases several hours elapsed before killing occurred, but when the rats were placed back into their own familiar home cages killing occurred in all instances with very little delay. Thus, these experiments by Karli demonstrate that a rat has to have some sense of familiarity with the environment with which it is in before it will kill in that environment.

The amount of information on the domestic rat's predatory or murcidal reaction is now fairly sizeable and many other variables besides that of environmental familiarity have been investigated. As of this date, however, very little has appeared in the scientific literature on the predatory behavior of another

56   R. H. POLSKY

commonly studied laboratory rodent, the golden hamster. Knowing the strong effect familiarity of the environment has on the rat's predatory response, it seemed desirable, as a start, to see if this factor affected the hamster in the same way. The study reported below, then, investigated the effects of a novel environment and of qualitatively different types of environments on the predatory behavior of the hamster.

METHOD

Ss were 5 male and 15 female golden hamsters (*M.a. auratus*) derived from a stock which had been selectively bred for their locust capturing ability. All Ss were laboratory born, weaned at 25 days of age and then housed individually in 7- $\times$ 7- $\times$ 9-in. sheet metal cages in which they lived for the duration of the experiment. A Perspex top covered each individual cage and a $\frac{1}{4}$ in. of sawdust covered each cage floor. Standard laboratory chow and water were provided *ad lib*. At the commencement of testing all Ss were approximately 60 days old and all had met the criterion of a successful capture when initially tested at 40 days of age.

To assure that the 20 selected Ss were reliable captors, all were given the additional opportunity to capture a locust in their own home cage on the day before the start of the testing regime. Those Ss which failed to meet the criterion of capture within 1 min. after prey introduction were discarded.

Testing was conducted once daily and was carried out over seven successive days. This consisted of lifting S out of its own home cage in a coffee mug and either putting it back into its own home cage (Test Day 1) or into a novel environment (Test Days 2 to 5). The novel environment consisted of a cage identical in all respects to S's own home cage except that it had been freshly cleaned prior to a test with a mild detergent and a new layer of sawdust had been inserted. For testing purposes four such identical novel environments were used. After the last test in the novel environment on Test Day 5 the 15 fastest captors were selected out and divided into three matched groups of five each. Subsequently, on Test Days 6 and 7 Ss in the first group were removed from their home cage and tested for prey capture in a cage in which a single female hamster had lived for approximately 2 mo. The second group was tested in a cage in which approximately two dozen locusts had lived for a period of 2 wk. and the third was tested in a neutral cage, i.e., a cage which had been freshly cleaned. The three test cages, although differing in their olfactory properties, were nevertheless identical to S's own home cage and to the test cages in which testing took place on Test Days 2 to 5.

Immediately after being transferred from its own home cage and placed in a test cage a locust was introduced through a 1-in. hole in the cage top. Tests were terminated after a successful capture occurred (defined as a hold on the locust with the forepaws for at least 15 sec.), and if S failed to capture after 15 min., it was then removed and returned to its own home cage. Latencies to capture were recorded on a stop watch and all tests were conducted during the dark phase of a reversed light-dark cycle.

The prey employed were active third instar locust nymphs (*Locusta migratoria*). All locusts were approximately $\frac{1}{2}$ in. in length and were derived from a culture maintained by the author.

RESULTS AND DISCUSSION

Every S met the pretest criterion of a successful capture within one minute on the day prior to test commencement. Capture in all cases occurred in a swift and efficient manner and was invariably accomplished by several quick nips to

the anterior end of the locust followed by seizure with the mouth and then grasp with the forepaws. The median latencies to capture on Test Day 1 (home cage) and on Test Days 2 to 5 are presented graphically in Fig. 1. Latencies to capture on Test Day 1 and Test Day 2 differ significantly ($p < .001$, Mann-Whitney U test) and further, a significant decrease in latency to capture occurred with repeated testing in the novel environment ($p < .001$, Friedman two-way analysis of variance). Latency to capture for those Ss tested in either the hamster-soiled cage, the locust-soiled cage or neutral cage on Test Days 6 and 7 appear in Fig. 2. Latency scores for the two test sessions have been combined and inspection shows that the Ss tested in either the hamster-soiled or neutral cage had a shorter latency to capture than those Ss tested in the locust-soiled cage. This difference, however, falls short of statistical significance ($F = 1.37$, $df = 2/8$, $p > .05$).

Qualitative difference, however, existed in the method of capture in each of the three cage conditions. Ss tested in the hamster-soiled and neutral cages exhibited a greater tendency to pursue the prey after detecting it, whereas Ss tested in the locust-soiled cage showed no such pursuit behavior and captured only if the locust happened to hop directly into it or if it happened to stumble upon the locust during cage exploration.

The results of this study clearly demonstrated that familiarity with the environment is one variable that can significantly affect hamster predatory behavior. Experienced hamster captors taken from their home cage and placed in a novel environment showed a significantly greater latency to capture. However, a hamster's reactivity to the effects of novelty probably habituated with repeated testing in the novel environment and this in turn explains the decreased latency with repeated testing. This finding is not surprising for it is concordant with
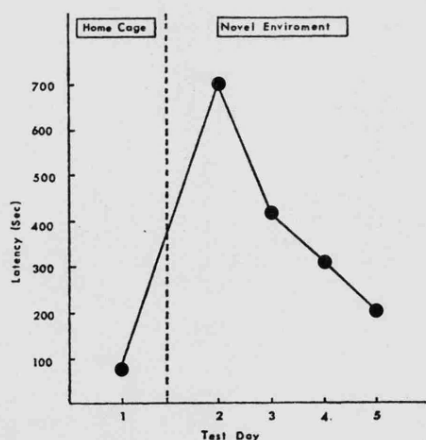
FIG. 1. Median latency to capture in the home cage and novel environment
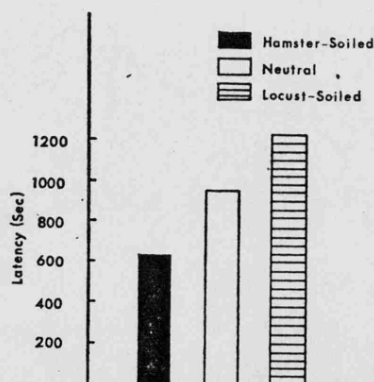
FIG. 2. Median latency to capture in three different test environments

58   R. H. POLSKY

those studies which examined the effects of a novel environment on frog killing and mouse killing by rats.

On the other hand, the relatively high latency to capture for those Ss tested in the locust-soiled cage probably stems from the fact that they had difficulty in locating the prey in an environment saturated with the smell of locusts. Hamsters probably depend heavily on their sense of smell to capture locusts and the use of olfaction in detecting prey is probably most effective only when a hamster can discriminate the olfactory characteristics of the prey from the background in which an encounter occurs. Hence, in the locust-soiled cage, the odor of the locust probably blended with the odor of the cage thus effectively camouflaging it from the hamster. However, when tested in an environment in which prey detection could readily be made, such as the types found in the hamster-soiled cage and neutral cage, capture was more likely to occur with a shorter latency mainly because a hamster had a greater chance of detecting the prey through olfaction. The qualitative differences in the behavior certainly make this explanation plausible. The reason why significant quantitative differences were not achieved could stem from the design of the experiment (Ss could have been tested under all three conditions in balanced order rather than separate groups tested under only one condition), the small sample size, or the small size of the testing compartment, i.e., Ss had a fairly good chance of locating the prey through random movement. The fact remains that most hamsters tested in the locust-soiled cage did eventually capture (four out of five), albeit with a greater latency, and this further suggests that capture of locusts by hamsters is under the control of several sense modalities and not just olfaction alone.

REFERENCES

AVIS, H. H., & TREADWAY, J. T. Mediation of rat-mouse interspecific aggression by cage odor. *Psychon. Sci.*, 1971, 22, 293-294.

BAENNINGER, R., & ULM, R. Overcoming the effects of prior punishment on interspecific aggression in the rat. *J. comp. physiol. Psychol.*, 1969, 69, 628-635.

DeSISTO, M. J., & HUSTON, J. P. Effect of territory on frog killing by rats. *J. gen. Psychol.*, 1970, 83, 179-184.

KARLI, P. The norway rat's killing response to the white mouse: an experimental analysis. *Behaviour*, 1956, 10, 81-101.

MILEY, W. M., & BAENNINGER, R. Inhibition and facilitation of interspecies aggression in septal lesioned rats. *Physiol. & Behav.*, 1972, 9, 379-384.

Hunger, Prey Feeding, and Predatory Aggression

RICHARD H. POLSKY[1]

University of Leicester,
Department of Psychology,
Leicester, England

Research on mammalian predatory aggression is reviewed with special attention being paid to the effects hunger and prey feeding have on the development and maintenance of the killing response. The findings are dichotomized into those which suggest a positive relationship between these two variables and killing, and those which negate a relationship. Those findings which suggest no relationship are drawn from the neurophysiological literature as well as from research which shows that experienced killers will kill in surplus, that the act of killing does not potentiate feeding, that nonkillers cannot be induced to kill through starvation, that experienced killers may not eat the prey after their first kills, and that experienced killers do not have to feed on the prey in order to maintain the killing response. These findings suggest that killing is self-reinforcing and studies are reviewed which buttress this belief. Studies which support the view that hunger, feeding, and killing are positively related come from research in which naive animals were either starved or fed dead prey prior to the initial test for prey killing. It was concluded that hunger and feeding are not needed in order to maintain the killing response in the experienced killer, but both can serve as potentiators for the induction of killing in the naive subject. Implications and limitations of this conclusion were then briefly discussed.

Research within the last two decades on the now well-studied phenomenon of rodent predatory aggression has produced, over-all, inconsistent findings concerning the roles hunger and prey feeding play in the development and maintenance of the killing response. Karli (1956), for example, in his pioneer study, concluded that hunger played only a partial role, and likewise the findings of Heimstra and Newton (1961), Whalen and Fehr (1964), and Heimstra (1965) have been equivocal in nature. On the other hand, others claimed the relationship is unclear (Moyer, 1968) while others have outrightly

81

denied any relationship between killing and hunger (Karli, Vergnes, and Didiergeorges, 1969). Still others have suggested that killing, prey feeding, and hunger relate to one another only in certain circumstances (Paul, 1972; Paul, Miley, and Mazzagatti, 1973). Further conflicting opinion comes from the recent review of O'Boyle (1974) who cogently argued that a positive relationship between prey feeding and killing does in fact exist.

Theoretically, it would be desirable to clarify the relationship in view of the widespread interest behavioral scientists have in the phenomenon of predatory aggression. First, if hunger induced killing and caused a predator to feed on the prey which it killed, then this would be one basis on which to separate out predatory aggression from the other types of aggression (O'Boyle, 1974, or see Moyer, 1968). Second, if hunger, prey feeding, and killing were related, then a fairly parsimonious explanation for the killing response could be made; i.e., predators kill because they are hungry, or they kill so that they can feed on what they killed (e.g., the prey). Alternatively, if there was no association between hunger, feeding, and killing, or a weak association, then other factors would have to be postulated to explain the motivational basis of killing. This critique will, therefore, attempt to reform and systematize the findings, mainly from the rodent literature, pertinent to this issue. In addition, relevant findings from other mammalian species will be considered for the sake of breadth and for comparative purposes.

FUNCTIONAL ASPECTS OF THE KILLING RESPONSE

Functionally, it is not difficult to discern the value of predatory killing; the behavior in all likelihood is primarily concerned with food procurement. Labeling it as a "food getting" behavior seems quite appropriate (Denny and Ratner, 1970) for it is known that even laboratory predators will eat the prey after a kill if given the opportunity. For example, experienced rat killers will eat the frogs and mice they kill (Bandler and Moyer, 1970; Paul, 1972; Paul and Posner, 1973; Thorne, Aaron, and Latham, 1973), and likewise cricket killing by mice is often followed by consumption (Thomas, 1969, 1972). Because of the obvious functional value, and because of the close sequential relationship between killing and eating, one might well conclude that these two events were related or one caused the other, or perhaps even be tempted to hypothesize a direct relationship between the tendency to kill, the tendency to feed, and a predator's level of hunger.

EVIDENCE WHICH NEGATES THE RELATIONSHIP BETWEEN HUNGER, PREY FEEDING, AND KILLING

However, as might be expected, the relationship between the killing of prey, the consumption of it, and hunger is not as straightforward and simple

as it might hypothetically seem. To understand this, take first the case of the animal who has had some prior experience with the prey. This experience need not only mean the experience of a successful kill but also the experience of not killing even though the prey was readily available. For such animals it seems as though the motivation to kill is independent of the need for food or the tendency to feed. This belief is supported by the following observations:

(1) *Predators have been known to kill far more prey then they need in order to satisfy their food requirements.* Such surplus killing has been documented in the Order Carnivora by Kruuk (1972) for canids and hyaenas, by Schaller (1972) for felids, by Rasa (1973) for viverrids, and another good example of killing in surplus can be in the raids and killing 'orgies' by certain canids on domestic livestock. In the Order Rodentia, Boice and Schmeck (1968) reported that the carnivorous grasshopper mouse will kill up to 40 crickets within a period of 2 hr, and DeSisto and Huston (1970) noted that domestic rats will kill as many as 30 frogs in rapid succession. Presumably then, predators are capable of killing far more prey then they could eat or would need to eat in order to satiate their hunger drive.

(2) *Prey killing will remain stable and constant in form even if a predator is denied the opportunity to feed on the prey which it has killed.* Myer (1967, 1969, 1971) has repeatedly demonstrated this in several of his studies with mouse-killing rats. According to Myer the act of killing is self-reinforcing in itself and reinforcing a rat by allowing it to feed on the mouse is not needed in order to maintain the behavior. The ethologist Leyhausen (1973) also noted that "once established, the killing bite will continue to develop its own appetite."

(3) *Experienced nonkillers cannot be induced to kill through starvation.* For example, Karli (1956) found that rats which never killed mice could not be made to do so even if subjected to extreme food deprivation. In fact, Karli reported that some of his rats starved to death in the presence of the prey. Likewise, Kuo (1930) in his classic study with cats reported that hunger had little effect on the rat killing response of nonkillers.

(4) *A predator after its first few kills may not consume the prey which it has killed.* Paul, Miley, and Baenninger (1971) reported that, initially, rats occasionally showed hesitancy about eating the prey. Karli (1956) also found that after the first few kills rats tended not to eat the mice or eat only after a great delay. With deer mice, Thomas (1971) found that the interval between killing and eating was often several minutes. Moreover, Leyhausen notes that consumption of the prey will not automatically follow a kill. According to Leyhausen, a predator has to learn the 'connection' between killing and eating. Therefore, it seems that these two behaviors are unrelated at first but subsequently become sequentially linked through the process of association.

(5) *Several variables which influence the probability of eating have been found to have little effect on prey killing.* For example, it is well-known that whether hungry or not an experienced mouse killer will kill if given the

84   RICHARD H. POLSKY

opportunity (initially Karli, 1956, and since then many others). Further, Paul, Miley, and Baenninger (1971) reported that water deprivation had little influence on the incidence of mouse killing (if thirsty, the probability of mouse killing should be low as it is with eating), and subsequently Paul (1972) found that the severity of food deprivation (75% ad lib. feeding weight versus 90% ad lib. feeding weight) and the time of testing in relation to the regular feeding hour (consumption of food and the probability of eating are highest at an animal's regular scheduled feeding time) had negligible effects. If killing and hunger were related, then a rat should be more likely to kill the hungrier it was and also if it was tested at the time it regularly fed.

(6) *The act of killing does not potentiate prey feeding.* If killing and feeding were related then a predator should show a greater inclination to feed on prey which itself had killed as opposed to prey which it had not killed. However, Paul and Posner (1973) found that rats presented dead prey which they themselves had not killed were just as likely to feed on such prey as those rats which were allowed to feed on prey which they themselves had killed. Further, the act of killing does not signal or serve as a cue to the predator to begin eating the prey which it has killed. Rats given the choice between a piece of chocolate and the prey immediately after a kill were just as likely to eat the chocolate as they were the prey (Paul and Posner, 1973).

(7) *Different anatomical sites in the brain govern eating and killing.* For instance, King and Hoebel (1968) reported that electrical stimulation in several sites of the rat's hypothalamus would elicit killing but not eating. In the study of Panksepp (1971) the reverse was found (i.e., stimulation which elicited eating would not elicit killing). In addition, it has been reported that stimulation of a rat's lateral hypothalamus will produce intensive oral activities, which resemble eating, but never attack and killing (Karli, Vergnes, and Didiergeorges, 1969). In another study, using cats, Hutchinson and Renfrew (1966) found that, although attack and killing could be elicited from the same hypothalamic sites, different intensities were required for each of the behaviors; attack required more intense stimulation for its elicitation than did eating.

Further, an intensive research program by Flynn and associates (reviewed in Flynn, 1967, or Flynn, Vanegas, Foote, and Edwards, 1970) has produced conclusive evidence indicating that attack, killing, and feeding are neurophysiologically distinct. Granted, Flynn argued, the findings of Hutchinson and Renfrew (cited above) are correct in that they substantiate the fact of definitive areas within the hypothalamus which, when stimulated, will elicit both attack and feeding. However, according to Flynn, they still do not obviate the likely possibility that different sites may also be involved. Like several others he drew on evidence which shows that stimulation to a particular hypothalamic site, known to elicit attack and killing, will not elicit feeding. Five examples are presented to support this contention. First, he cites one of his early studies (Wasman and Flynn, 1962) in which cats were

stimulated in a hypothalamic area known to reliably elicit attack, but only in the presence of a dish of food (no prey was present). Under these circumstances, Flynn found that his cats would sniff at the food, savagely bite it, and then prowl around the cage (apparently, an appetitive search for the prey) with the food often falling out of the mouth. In no instance was the food ever ingested. Second, Flynn found that, if stimulation which elicited attack was prolonged beyond the attack itself, this would not induce a cat to start feeding on the prey. The underlying assumption of this finding being, namely, that if killing and feeding were related neurophysiologically, then the same site which elicited killing should have likewise elicited eating. Third, Flynn reported an experiment in which cats were presented either horsemeat or an- anesthetized rat concomitant with stimulation to several selected sites in the hypothalamus at different levels of intensity. The intensity of stimulation in this experiment was raised in increments until a subject either ate the horsemeat or attacked the rat. Flynn found, in five of his seven cats tested, that stimulation which elicited attack would not elicit feeding. Moreover, the more intense the stimulation was (it ranged from .10 to .60 mA) the more readily attack was elicited, and in the two subjects in which attack and eating were elicited from the same sites, more intense stimulation was needed to elicit eating than attack. Fourth, Flynn cited an experiment in which cats were stimulated both in the presence of horsemeat and a rat. During all presentations, however, the food was always placed closer than the rat to the cat for it was known from previous research (Hutchinson and Renfrew, 1966) that whether a cat would attack or feed depended, to an extent, on which object was closer. Thus, in this situation, with stimulation to the same site, one would have expected most cats to eat rather than attack, assuming that attack and eat were both under the control of the site being stimulated. However, the results clearly showed that rather than eat, most cats attacked. Last, Flynn noted that if cats were continuously starved for 3 days, given food and then shortly afterwards a rat, they would break off eating to attack the rat when stimulated. Taken together, the evidence drawn from these five examples suggests that stimulation in certain sites of the hypothalamus will evoke predatory attack (of the quiet biting type) but not eating.

Additional weight for the theory of seperate neural centers for killing and eating has come from the research of Karli and associates (cited in Karli, Vergnes and Didiergeorges, 1969). These authors claimed that they successfully abolished both killing and eating in rats with bilateral lesions in the hypothalamus; however, they subsequently found that the recovery of killing invariably preceded the recovery of eating. According to these authors, "the question arises as to whether or not hunger or some selective appetite are essential factors in building up the motivational state underlying the killing response. We feel that this is not the case for the following reason: if the animal bearing lateral hypothalamic lesions....recovers oriented behavioral activities, the recovery of the killing response invariably preceded....the

86   RICHARD H. POLSKY

recovery of feeding behavior; the reappearance of interspecific aggression may
thus occur even though that animal still happens to be in a state of complete
adipsia and aphagia, never eating anything of the mouse it kills." The
interested reader should consult Roberts and Kiess (1964) for additional
evidence that different anatomical sites in the brain govern the eating and
killing responses.

KILLING AS A SELF-REINFORCER

Thus, what the evidence reviewed so far suggests is that prey killing in
the experienced predator is governed by a motivation which is separate and
distinct from the motivation which governs feeding. This being the case, a
number of investigators have reported experiments which show that the act of
killing itself can serve as a reinforcer. Myer and White (1965), and Kilby,
Moore, and Harris (1973), for example, have demonstrated that the oppor-
tunity to kill mice or frogs was a sufficiently strong incentive to main-
tain discrimination learning by rats. In both of these studies, rats which
were experienced killers learned to enter the arm of a T-maze that led to prey
which they could kill. In similar fashion, Roberts and Kiess(1964) reported
that cats during stimulation of the hypothalamus learned to enter the arm of
a Y-maze in order to gain access to a rat which they could kill. Rats have
even been taught the operant response of bar pressing in a Skinner box for
the delivery of a reward—a mouse which could be killed (Van Hemel, 1972;
Van Hemel and Myer, 1971) or a frog which could be killed (DeSisto and
Huston, 1971).

If the act of killing is reinforcing in its own right and further has
motivational properties of its own, then one would eventually expect the
behavior to satiate after it has been performed so many times. Kulkarni
(1968) has gathered evidence which shows that this is in fact what happens.
In his experiment three groups of 12 experienced killers were presented seven
mice in succession at intervals of 15, 30, or 60 min, respectively. Kulkarni
found that half the rats in the 15-min group stopped killing during testing as
opposed to only three in the 30-min group, and only one in the 60-min group.
Thus, whether or not a rat stopped killing seemed to depend on the interval
between presentations. Kulkarni argued that the waning of mouse killing was
due to the exhaustion or habituation of the behavior and he used the term
"action specific exhaustibility" to explain his findings.

Additional evidence along these lines has come from Moyer (1971) who
found that the killing behavior of an experienced rat killer would satiate if it
was presented between 5 and 10 mice in succession at intervals of 1 min each.
Moyer observed that when this occurred a satiated rat would allow an

exploring mouse to walk over it and even nestle with it. Further, Moyer noted that a rat's tendency to kill frogs also waned after its mouse-killing behavior was satiated, thus suggesting that both the killing response to frogs and mice were governed by a similar motivation.

EVIDENCE WHICH SUPPORTS THE RELATIONSHIP BETWEEN HUNGER, PREY FEEDING, AND KILLING

Up to now the discussion has been solely concerned with those animals that were regarded as "experienced"; that is, experienced in terms of killing or not killing. This distinction was necessary for it helps explain some important data recently collected by Paul and colleagues (Paul, 1972; Paul, Miley, and Baenninger, 1971). What these authors found was that food deprivation served to greatly facilitate the initiation of mouse killing in naive rats. Hunger, in one study (Paul et al., 1971) was induced through a 2-wk period of cyclic food deprivation prior to the initial mouse-killing test, and in another study (Paul, 1972) through continuous starvation for 7 days. In fact, it was found that just the experience of being maintained on the cyclic schedule (and later tested when food satiated) increased the chances of killing considerably. These findings are important and above all reliable for they have been replicated by these authors in a series of experiments (also see Paul, Miley, and Mazzagatti, 1973).

At first they may appear discrepant with the earlier-cited work, and especially with the finding of Karli (1956). However, Paul and her colleagues argued that if one attempts to explain the differential effects of starvation in terms of the past experience of the animal being starved, then their findings do not conflict with Karli's. Karli, they asserted, exposed his rats to the potential prey both before and during the course of food deprivation while in their experiments rats were first exposed to the mice only after a substantial period without food. Accordingly, then, such prior experience "interfered with subsequent killing when the rats were quite hungry" (Paul, 1972). More to the point, what is inferred is that the prior exposures Karli's animals received (when they were food satiated) reinforced habits incompatible with killing, or simply strengthened the habit of not killing per se. These habits, in turn, interfered with and suppressed whatever potentiating effects starvation might have had.

Paul (1972) conducted an elegant experiment to test this hypothesis. Rats (all naive) were assigned to four groups and housed either individually or with the prey species (a single mouse). Further, half the rats in each group were continuously starved for 7 days prior to the first mouse killing test, or maintained for 7 days on a cyclic feeding regimen. Thus, half the rats were exposed to the prey during the course of starvation and half were not. When

tested, those subjects which were housed with the prey killed in significantly fewer instances compared to those subjects which were starved but without such exposure. Moreover, rats from both the exposed and nonexposed groups which were continuously starved showed a greater incidence of killing than those subjects which were maintained on the cyclic schedule. Further, Paul let all subjects feed ad lib. for 3 days after the last mouse-killing test. They were then subsequently tested and it was found that every rat which killed when hungry continued to kill when food satiated. Thus, hunger did not seem to be a necessary condition to maintain killing initially induced through starvation.

Evidence suggesting some relationship between feeding and killing has also come from the work of Paul and associates (see Paul and Posner, 1973). In one experiment these authors starved naive rats for 4 days and then proffered to them a dead mouse (killed by another rat) which they were allowed to feed on for 30 min. Mouse killing tests were then conducted 30 min later and compared to those of rats which were tested first without prior eating. These eat-first subjects showed a greater incidence of killing (76% vs 51%) and killed with a significantly shorter latency. This finding thus suggests that eating dead prey potentiates killing in the naive predator.

Studies conducted in this author's laboratory (Polsky, in preparation) with another rodent species, the golden hamster, also suggest that hunger and prior feeding on dead prey are strong potentiators of predatory aggression. In several experiments naive hamsters were continuously starved for 3, 4, or 5 days and when first tested for locust capture, deprived subjects captured significantly more often than food-satiated controls. In another experiment naive hamsters were allowed to feed on· dead locusts prior to their first exposure to a live locust. Again this treatment significantly increased the chances of capture. Prior starvation, however, seems to have little effect on this species. In one experiment, hamsters were starved early in life (prior to weaning) and then tested shortly after weaning when food satiated. Compared to controls these subjects showed no significant difference in the incidence of capture. This finding thus differs from the results obtained by Paul et al. (1971) with rats. Other studies have also been conducted by this author on the hitherto· neglected phenomenon of hamster predatory aggression. One report has already been published (Polsky, 1974) and others in preparation are concerned with the effects of age and experience, the reinforcing effects of eating after capture, priming, water deprivation, prey size, social isolation, and genotype.

CONCLUSIONS

In summary, then, re-formation of the evidence suggests that a subject's past experience with the prey is of paramount importance in determining the

TABLE 1

The Effect of Hunger and Prey Feeding on Predatory Aggression

Variable	Investigator and date	Effect	Predator	Prey
Feeding on prey subsequent to kill	Karli, 1956; Myer, 1964, and many others	Negligible	Rats (experienced)	Mice
Prior feeding on dead prey	Paul, 1972; Paul and Posner, 1973	Facilitory	Rats (naive)	
	Polsky (in preparation)	Facilitory	Hamsters (naive)	Locusts
Food deprivation				
Continuous	Karli, 1956	Negligible	Rats (nonkillers)	Mice
	Paul, 1972	Facilitory	Rats (naive)	Mice
	Polsky (in preparation)	Facilitory	Hamsters (naive)	Locusts
Cyclic	Whalen and Fehr, 1964	Facilitory	Rats (naive)	Mice
	Paul et al., 1971			

effects hunger and prey feeding have on predatory aggression. It seems that these two variables have relatively little influence on the maintenance of killing in the experienced killer but, on the other hand, a positive influence on the initiation of killing in the naive subject. The findings which warrant this conclusion are summarized in Table 1.

The fact that prior dead feeding has positive consequences, and that the drive for killing and that of hunger become separate through experience makes sense, biologically speaking.[2] Feeding on dead prey or partially killed prey brought in by the mother could be one means by which the young inexperienced predator familiarizes itself with novel prey. Prey-killing responses could then be practiced and the young predator could learn that what it was feeding on was in fact an edible and palatable food substance. Observations do, in fact, substantiate the belief that a mother often assists in introducing the young to their first prey; this happens, for example, in domestic cats (Ewer, 1968), tigers (Schaller, 1967), cheetahs (Eaton, 1970; Kruuk and Turner, 1967), grasshopper mice (Ruffer, 1966), and golden hamsters (author's personal observations).

[2]In the more specialized predators, such as the Carnivora, experience may not be needed to separate out the killing and hunger drives. Due to the selective pressures placed on the killing response in those species that depend primarily on prey as a source of food, it is conceivable that the killing drive has become emancipated from the hunger drive. Lorenz (1966), Leyhausen (1973), and other ethologists have argued strongly for this point.

90   , RICHARD H. POLSKY

The fact that an experienced predator will continue to kill even though it may not be hungry is one means by which it could assure itself, or its companions (in the case of group-living predators), of an adequate supply of food. Prey which was not eaten after the kill could be passed on to a conspecific or cached for later consumption. The sharing of prey could be a means of maintaining organization within a social group, and caching could prove advantageous to predators who hibernate or to predators who do not . readily have access to prey the year round (see Ewer, 1968, pp. 54-55 for a brief discussion on this point, or see Kruuk, 1972).

Further, one must realize that many other factors besides hunger and prior prey feeding have been found to facilitate the onset of killing in the naive subject. These include the genotype of the individual (Butler, 1973), prior competitive experience (Heimstra and Newton, 1961), social isolation (Bernstein and Moyer, 1970; Johnson, DeSisto, and Koenig, 1972; Kuo, 1960), type of prey species used (Bandler and Moyer, 1970), rank in a dominance hierarchy (Leyhausen, 1973), observational learning (Kuo, 1930), and the physiological changes brought on by pregnancy and lactation (Flandera and Novakova, 1971).

Lastly, another shortcoming of the majority of studies reviewed in this paper stems from the fact that most researchers have assumed that hunger is a unitary concept when in fact it is not (Deutsch, 1971). Many specific hungers exist (Rozin and Kalat, 1971) and it could well be that a rat, for example, that is apparently well-satiated on laboratory chow still has a specific hunger for mice (or perhaps some specific part of a mouse, such as the brain); hence it could be just this type of hunger and not hunger in a general sense which drives it to kill. The fact that eating often follows a kill in the predator satiated on laboratory chow certainly does suggest that a specific hunger may be present; however, few researchers have taken this variable into account as a causal factor. Because of this, additional research is needed to ascertain if a specific hunger for mice (or frogs) exists, and if so, what effect it has on the killing response. Until then one must remain somewhat skeptical of any theory concerned with the relationship between hunger, prey feeding, and killing, or on the motivation for killing in general.

REFERENCES

Bandler, R., and Moyer, K. E. (1970). Animals spontaneously attacked by rats. *Commun. Behav. Biol.* 5, 177-181.

Bernstein, H., and Moyer, K. E. (1970). Aggressive behavior in the rat: Effects of isolation and olfactory bulb lesions. *Brain Res.* 20, 75-84.

Boice, R., and Schmeck, R. R. (1968). Predatory behaviors of grasshopper mice (*Onychomys leucogaster*). *Amer. Zool.* 8, 79.

Butler, K. (1973). Predatory behavior in laboratory mice: Sex and strain comparisons. *J. Comp. Physiol. Psychol.* 85, 243-249.

Denny, M. R., and Ratner, S. C. (1970). "Comparative Psychology." Homewood, IL: Dorsey.

DeSisto, M. J., and Huston, J. P. (1970). Effect of territory on frog killing by rats. *J. Gen. Psych.* 83, 179-184.

DeSisto, M. J., and Huston, J. P. (1971). Aggression and reward from stimulating common sites in the posterior lateral hypothalamus of rats. *Commun. Behav. Biol.* 6, 295-306.

Deutsch, J. A. (1971). Appetitive motivation. *In* J. L. McGaugh (Ed.), "Psychobiology: Behavior from a Biological Perspective," pp. 99-128. London: Academic Press.

Eaton, R. L. (1970). The predatory sequence with emphasis on killing behavior and its ontogeny in the cheetah *(Acinonyx jubatus* Schreber). *Z. Tierpsychol.* 27, 492-504.

Ewer, R. F. (1968). "Ethology of Mammals." London: Logos Press Ltd.

Flandera, V., and Novakova, V. (1971). The development of interspecies aggression of rats towards mice during lactation. *Physiol. Behav.* 6, 161-164.

Flynn, J. P. (1967). The neural basis of aggression in cats. *In* D. C. Glass (Ed.), "Neurophysiology and Emotion," pp. 40-60. New York: Rockefeller Univ. Press and Russel Sage Found.

Flynn, J. P., Vanegas, H., Foote, W., and Edwards, S. (1970). Neural mechanisms involved in a cat's attack on a rat. *In* R. Whalen, R. F. Thompson, M. Verzeano, and N. Weinberger (Eds.), "The Neural Control of Behavior," pp. 135-173. New York: Academic Press.

Heimstra, N. W. (1965). A further investigation of the development of mouse killing in rats. *Psychon. Sci.* 2, 179-180.

Heimstra, N. W., and Newton, G. (1961). Effects of prior food competition on the rat's killing response to the white mouse. *Behaviour* 17, 95-102.

Hutchinson, R. R., and Renfrew, J. W. (1966). Stalking attack and eating behaviors elicited from the same site in the hypothalamus. *J. Comp. Physiol. Psychol.*, 61, 360-367.

Johnson, R. N., DeSisto, M. J., and Koenig, A. B. (1972). Social and developmental experience and interspecific aggression in rats. *J. Comp. Physiol. Psychol.* 79, 237-242.

Karli, P. (1956). The Norway rat's killing response to the white mouse: An experimental analysis. *Behaviour* 10, 81-101.

Karli, P., Vergnes, M., and Didiergeorges, F. (1969). Rat-mouse interspecific aggressive behaviour and its manipulation by brain ablation and by brain stimulation. *In* S. Garattini and E. B. Sigg (Eds.), "Aggressive Behaviour," pp. 47-55, Amsterdam: Excerpta Medica Foundation.

Kilby, M. M., Moore, J. W., and Harris, R. T. (1973). Effects of Delta-9 tetrahydrocannabinol on appetitive and aggressive rewarded maze performance in the rat. *Physiol. Psychol.* 1, 174-176.

King, M. B., and Hoebel, B. G. (1968). Killing elicited by brain stimulation in the rat. *Commun. Behav. Biol.* 2, 173-177.

Kruuk, H., and Turner, M. (1967). Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. *Mammalia* 31, 1-27.

Kruuk, H. (1972). Surplus killing by carnivores. *J. Zool.* 166, 233-244.

Kulkarni, A. S. (1968). Satiation of instinctive mouse killing by rats. *Psychol. Rec.* 18, 385-388.

Kuo, Z. Y. (1930). The genesis of the cat's responses to the rat. *J. Comp. Psychol.* 11, 1-35.

506.

92   RICHARD H. POLSKY

Kuo, Z. Y. (1960). Studies on the basic factors in animal fighting: VII. Inter-species coexistence in mammals. *J. Genet. Psychol.* 97, 211-235.

Leyhausen, P. (1973). On the function of the relative hierarchy of moods (as exemplified by the phylogenetic and ontogenetic development of prey-catching in carnivores). *In* K. Lorenz and P. Leyhausen (Eds.), "Motivation of Human and Animal Behavior," pp. 144-247. London: Van Nostrand Reinhold.

Lorenz, K. (1966). "On Aggression." New York: Harcourt, Brace and World.

Moyer, K. E. (1968). Kinds of aggression and their physiological basis. *Commun. Behav. Biol.* 2, 65-87.

Moyer, K. E. (1971). A preliminary physiological model of aggressive behavior. *In* B. E. Eleftheriou and J. P. Scott (Eds.) "The Physiology of Aggression and Defeat," pp. 223-263. London: Plenum Press.

Myer, J. S. (1967). Prior killing experience and the suppressive effects of punishment on the killing of mice by rats. *Anim. Behav.* 15, 59-61.

Myer, J. S. (1969). Early experience and the development of mouse killing by rats. *J. Comp. Physiol. Psychol.* 67, 46-49.

Myer, J. S. (1971). Experiences and the stability of mouse killing by rats. *J. Comp. Physiol. Psychol.* 75, 264-268.

Myer, J. S., and White, R. T. (1965). Aggressive motivation in the rat. *Anim. Behav.* 13, 430-433.

O'Boyle, M. (1974). Rats and mice together: The predatory nature of the rat's mouse-killing response. *Psychol. Bull.* 81, 261-269.

Panksepp, J. (1971). Aggression elicited by electrical stimulation of the hypothalamus in albino rats. *Physiol. Behav.* 6, 321-329.

Paul, L. (1972). Predatory attack by rats: Its relationship to feeding and type of prey. *J. Comp. Physiol. Psychol.* 78, 69-76.

Paul, L., Miley, W. M., and Baenninger, R. (1971). Mouse killing by rats: Roles of hunger and thirst in its initiation and maintenance. *J. Comp. Physiol. Psychol.* 76, 242-249.

Paul, L., Miley, W. M., and Mazzagatti, N. (1973). The social facilitation and inhibition of hunger-induced killing by rats. *J. Comp. Physiol. Psychol.* 84, 162-168.

Paul, L., and Posner, I. (1973). Predation and feeding: Comparisons of feeding behavior of killer and non-killer rats. *J. Comp. Physiol. Psychol.* 84, 258-264.

Polsky, R. H. (1974). Effects of novel environment on predatory behavior of golden hamsters. *Percept. Motor Skills.* 39, 55-58.

Polsky, R. H. (In prep). "The Ontogeny of Hamster Predatory Behavior." Ph.D. thesis, Univ. of Leicester, Leicester, England.

Rasa, O. A. E. (1973). Prey capture, feeding techniques, and their ontogeny in the African Dwarf mongoose, *Helogale undulata rufula. Z. Tierpsychol.* 32, 449-488.

Roberts, W. W., and Kiess, H. O. (1964). Motivational properties of hypothalamic aggression in cats. *J. Comp. Physiol. Psychol.* 58, 187-193.

Rozin, P., and Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychol. Rev.* 78, 459-486.

Ruffer, D. G. (1965). Sexual behavior of the Northern grasshopper mouse (*Onychomys leucogaster*). *Anim. Behav.* 13, 447-452.

Schaller, G. B. (1967). "The Deer and the Tiger." Chicago: Univ. Chicago Press.

Schaller, G. B. (1972). "The Serengeti Lion: A Study of Predator-Prey Relations." Chicago: Univ. Chicago Press.

Thomas, K. (1969). Predatory behavior in two strains of laboratory mice. *Psychon. Sci.* 15, 13-14.

Thomas, K. (1971). Predatory behavior in mice: Strain and sex comparisons. Paper presented to the Western Psychol. Assoc. Meeting. April, 1971.

Thomas, K. (1972). Selective breeding for fast and slow cricket-killing in laboratory mice. Paper presented at the meeting of the Animal Behav. Soc. June, 1972; Reno, Nevada.

Thorne, B. M., Aaron, M., and Latham, E. E. (1973). Effect of olfactory bulb ablation upon emotionality and muricidal behavior in four rat strains. *J. Comp. Physiol. Psychol.* 84, 339-344.

Van Hemel, P. (1972). Aggression as a reinforcer: Operant behavior in the mouse-killing rat. *J. Exp. Anal. Behav.* 17, 237-245.

Van Hemel, P., and Myer, J. S. (1970). Satiation of mouse killing by rats in an operant situation. *Psychon. Sci.* 21, 129-130.

Whalen, R. E., and Fehr, H. (1964). The development of the mouse killing response in rats. *Psychon. Sci.* 1, 77-78.

Wasman, M., and Flynn, J. P. (1962). Directed attack elicited from the hypothalamus. *Arch. Neurol.* 6, 220-227.

APPENDIX D

APPENDIX D

FURTHER READING

Listed below are publications which in most cases became available after the final draft of Chapter 2 had been written. The serious student should find them of value in pursuing his own research or reading.

Apfelbach, R. (1973). Olfactory sign stimulus for prey selection in polecats. Z. Tierpsychol. 33, 270 - 273.

Presents evidence which shows that polecats learn the smell of prey most readily between two and three months of age; i.e. argues for a sensitive period.

Berg, D. and Baenninger, R. (1974). Predation: Separation of aggressive and hunger motivation by conditioned aversion. J. Comp. Physiol. Psychol. 86, 601 - 606.

Rats were poisoned with lithium chloride after killing, or after eating prey. With this method killing and eating were suppressed independently, thus indicating that each of these behaviours have motivational properties of their own. See text, Chapter 2 Section 2.4b.6, for related studies.

Appendix D, continued.

Bernard, B.K. (1974). Frog killing (ranacide) in the male rat:

Lack of effect of hormonal manipulations. Physiol. Behav.

12, 405 - 408.

The findings suggest that frog killing is independent of

the direct effects of the male hormone testosterone.

Cain, D.P. and Paxinos, G. (1974). Olfactory bulbectomy and

mucosal damage: Effects on copulation, irritability and

interspecific aggression in male rats. J. Comp. Physiol.

Psychol. 86, 202 - 212.

Like other recent studies, this study demonstrated that

bulbectomy induced mouse killing is not entirely due to an

olfactory deficit per se, but rather to olfactory deficit

plus central nervous ablation. The evidence suggests that

bulbectomy induced mouse killing may be a form of irritable

aggression.

Eaton, R.L. (1974). The Cheetah: The Biology, Ecology and Behavior

of an Endangered Species. London: Van Nostrand Reinhold.

A general overview of cheetah behaviour and its relationship

to ecology. Topics include social organization, spacing,

aggression, predation and conservation.

Ginsburg, H.J. and Braud, W.G. (1971). A laboratory investigation

of aggressive behavior in the Mongolian gerbil (Meriones

unguiculatus). Psychon. Sci. 22, 54 - 55.

Reports gerbils housed individually attacked mice and rats

introduced into their home cage. Refers to it as interspecific

aggression, but makes no mention if the rats or mice were killed

or eaten.

Appendix D, continued.

Herrenkohl, L.R. (1974). Mouse killing in virgin, pregnant and

lactating rats. Physiol. Behav. 13, 171 - 173.

Found no difference in the incidence of killing among virgin,

pregnant and lactating rats. Suggests that differences may

have been obviated due to the low incidence of spontaneous

killing in the strain of the rats employed (Sprauge-Dawley).

Knutson, J.F. and Hynan, M.T. (1973). Predatory aggression and

irritable aggression: Shock - induced fighting in mouse-killing

rats. Physiol. Behav. 11, 113 - 115.

Attempted to delineate the relationship between irritable

aggression (shock-induced fighting) and predatory aggression.

Found that both killers and non-killers were as equally likely

to fight when shocked, regardless of intensity.

Krames, L., Milgram, N.W. and Christie, D.P. (1973). Predatory

aggression: Differential suppression of killing and feeding.

Behav. Biol. 9, 641 - 647.

Administered lithium chloride either after killing or after

eating and successfully suppressed each behaviour independently.

Further, differential recovery of killing and eating were obser-

ved. The findings are similar to those of Berg and Baenninger,

(1974).

Latham, E.E. and Thorne, B.M. (1974). Septal damage and muricide:

Effects of strain and handling. Physiol. Behav. 12, 521 - 526.

Found handling, post-operatively, in septal lesioned rats had

Appendix D, continued.

no effect on the killing response. Septal lesions, however,
increased the probability of killing in Long-Evans, but not
Sprauge-Dawley rats.

Myer, J.S. (1971). Some effects of noncontingent aversive stimu-
lation. In F.R. Bush (ed.), Aversive Conditioning and Learning.
pp. 469 - 536. London: Academic Press.
Myer reviews most of his research on shock-induced mouse killing
in rats.

O'Boyle, M. (1974). Rats and mice together: The predatory nature
of the rat's mouse killing response Psychol. Bull. 81, 261 -
269.
The first review to appear in the literature on predatory
behaviour in the domestic rat. Argues strongly for a distinc-
tion between intra-specific aggression and predation.

O'Boyle, M., Looney, T. and Cohen, P.S. (1973). Suppression and
recovery of mouse killing in rats following immediate lithium-
chloride injections. Bull. Psychon. Soc. 1, 250 - 252.
Suppressed mouse killing with lithium chloride injections.
Corroborates other recent findings.

Plotnik, R. (1974). Brain stimulation and aggression: Monkeys,
apes and humans. In R.L. Holloway (ed.), Primate Aggression,
Territoriality and Xenophobia: A Comparative Perspective.
London: Academic Press.
Concludes brain mechanisms for predation are innately organ-
ized in rats and cats.

Appendix D, continued.

Rifkin, R.J., Silverman, J.M., Chavez, F.T. and Frankl, G. (1974).
Intensified mouse killing in the spontaneously hypertensive
rat. Life Sci. 14, 985 - 992.
Reports that social isolation causes an increase in mouse
killing in hypertensive male rats.

Soane, I.D. and Clarke, B. (1973). Evidence for apostatic selection
by predators using olfactory cues. Nature, 241, 62 - 63.
Questionable if what these authors looked at was a form of
predatory behaviour.

Stern, P. and Igic, R. (1971). The role of olfaction in the rat's
killing response to the white mouse. Acta Biol. Iugosl. Serc.
Iugos, Physiol. Pharm. Acta. 7, 177 - 180.
A difficult publication to obtain but probably relevant to a
large body of literature.

Teleki, G. (1974). The Predatory Behavior of Wild Chimpanzees.
Lewisburg, Pa.: Bucknell Univ. Press.
Describes in detail the predatory habits of chimps on infant
baboons in the Gombe National Park.

Van Hemel, P.E. and Colucci, V.M. (1973). Effects of target movement
on mouse-killing attack by rats. J. Comp. Physiol. Psychol. 85,
105 - 110.
Tested naive rats with active mice or anaesthetized mice.
Found that rats killed anesthetized mice more
often, but active mice were attacked with shorter latencies.

Appendix D, continued.

Wnek, D.J. and Leaf, R.C. (1973). Effects of cholinergic

drugs on prey-killing by rodents. Physiol. Behav. 10,

1107 - 1113.

These authors studied the predatory reaction of hamsters

and found a low incidence of spontaneous mouse killing

(11%). Further, they failed to induce killing through

pilocarpine treatment. Perhaps they should have tried

a different prey species ?

BIBLIOGRAPHY

Adler, S. (1948). Origin of the golden hamster, Cricetus Auratus, as a laboratory animal. Nature. 162, 256 - 257.

Alberts, J.R. and Friedman, M.I. (1972). Olfactory bulb removal but not anosmia increases emotionality and mouse-killing. Nature. 238, 454 - 455.

Allee, W.C., Emerson, A.E., Park, O., Park, T., and Schmidt, K.P. (1949). Principles of Animal Ecology. London: W.B. Saunders.

Allen, D.L. and Mech, L.D. (1963). Wolves versus moose on Isle Royale. National Geographic Magazine. 123, 200 - 219.

Altmann, S. (1974), Baboons, space, time and energy. Amer. Zool. 14, 221 - 248.

Anton, B.S. and Bennett, T.L. (1972). Role of tactual-kinesthetic feedback in transfer of perceptual learning in the golden hamster. Psychon. Sci. 28, 157 - 158.

Aschoff, J., Figala, J., and Poppel, E. (1973). Circadian rhythms of locomotor activity in the Golden Hamster (Mesocricetus Auratus) measured with two different techniques. J. Comp. Physiol. Psychol. 85, 20 - 28.

Ashby, G.J. (1967). Locusts. In W. Lane-Petter, A.N.Worden, B.F. Hill, J.S. Patterson and H.G. Vevers (eds.), The UFAW Handbook: The Care and Management of Laboratory Animals. 3rd edition. London: E. & S. Livingstone Ltd.

Avis, H.H. and Treadway, J.T. (1971). Mediation of rat - mouse

interspecific aggression by cage odor. Psychon. Sci. 22, 293 - 294.

Baenninger, R. (1967). Contrasting the effects of fear and pain on

mouse killing by rats. J. Comp. Physiol. Psychol. 63,

298 - 303.

Baenninger, R. (1969). Independence of parturition and mouse-killing

by female rats. Psychon. Sci. 15, 144.

Baenninger, R. (1970). Suppression of interspecies aggression in the

rat by several aversive training procedures. J. Comp. Physiol.

Psychol. 70, 382 - 388.

Baenninger, L.P. and Baenninger, R. (1970). "Spontaneous" fighting

and mouse-killing by rats. Psychon. Sci. 19, 161.

Baenninger, R. and Miley, W.M. (1971). Day one castration effects

on aggressive and parental behavior of laboratory rats.

Amer. Zool. 11, 621.

Baenninger, R. and Ulm, R. (1969). Overcoming the effects of prior

punishment on interspecies aggression in the rat. J. Comp.

Physiol. Psychol. 69, 628 - 635.

Balagura, S. (1973). Hunger: A Biopsychological Analysis.

New York: Basic Books.

Bandler, R.J., Jr. (1969). Facilitation of aggressive behavior in

the rat by direct cholinergic stimulation of the hypothalamus.

Nature. 224, 1035 - 1036.

Bandler, R.J., and Chi, C.C. (1972). Effects of olfactory bulb

   removal on aggression: A reevaluation. Physiol. Behav. 8,

   207 - 211.

Bandler, R. and Moyer, K.E. (1970). Animals spontaneously attacked

   by rats. Comm. Beh. Biol. 5, 177 - 181.

Barnett, S.A. (1958). An analysis of social behaviour in wild rats.

   Proc. zool. Soc. Lond. 134, 107 - 152.

Barnett, S.A. (1963). The Rat: A Study in Behaviour. London: Methuen.

Beach, F.A. (1948). Hormones and Behavior. New York: Hoeber.

Beach, F.A. (1950). The snark was a boojum. Amer. Psychol. 5,

   115 - 124.

Beach, F.A. and Rabedeau, G. (1959). Sexual exhaustion and recovery

   in the male hamster. J. Comp. Physiol. Psychol. 52, 56 - 61.

Bernstein, H. and Moyer, K.E. (1970). Aggressive behavior in the

   rat: Effects of isolation and olfactory bulb lesions. Brain

   Res. 20, 75 - 84.

Blest, A.D. (1957). The function of eyespot patterns in the

   Lepidoptera. Behaviour. 11, 209 - 256.

Blossom, P.M. (1932). A pair of long-tailed shrews in captivity

   J. Mammology. 13, 136 - 143

Boice, R. (1973). Domestication. Psychol. Bull. 80, 215 - 230.

Boice, R. and Schmeck, R.R. (1968). Predatory behaviors of grass-

   hopper mice (Onychomys leucogaster). Amer. Zool. 8, 79.

Brain, P. (1972). Effects of isolation/grouping on endocrine function and fighting behavior in male and female golden hamsters (Mesocricetus Auratus Waterhouse). Behav. Biol. 7, 349 - 357.

Broadhurst, P.L.(1960). Experiments in psychogenetics. In H.J.Eysenck (ed.), Experiments in Personality. London: Routledge & Kegan Paul.

Bronson, G.W. (1966). Evidence of the lack of influence of early diet on adult food preferences in rats. J. Comp. Physiol. Psychol. 62, 162 - 164.

Bronson, G.W. (1968). The fear of novelity. Psychol. Bull. 69, 350 - 358.

Brower, L.P. and Brower, J.V.Z. (1964). Birds, butterflies and plant poisons: A study in ecological chemistry. Zoologica. 49, 137 - 159.

Brown, H.P. and Jenkins, M.M. (1962). A protozoon (Dileptus: Ciliata) predatory upon metazoa. Science. 36, 710.

Beukema, J.J. (1968). Predation by the three-spined stickle-back (Gasterosteus Aculeatus L): The influence of hunger and experience. Behaviour. 31, 1 - 126.

Bugbee, N.M. and Eichelman, B.S. (1972). Sensory alterations and aggressive behavior in the rat. Physiol. Behav. 8, 981 - 985.

Burghardt, G.M. (1964). Effects of prey size and movement on the feeding behavior of Lizards, Anolis carolmenis and Eumeces fasciatus. Copeia. 3, 576 - 578.

Burghardt, G.M. (1967). Chemical-cue preference of inexperienced

snakes : Comparative aspects. Science. 157, 718 - 721.

Burghart, G.M. (1969). Comprative prey-attack studies in newborn

snakes of the genus Thamnophis. Behaviour. 33, 77 - 114.

Burghardt, G.M. and Abeshaheen, J.P. (1971). Responses to chemical

stimuli of prey in newly hatched snakes of the genus Elaphe.

Anim. Behav. 19, 486 - 489.

Burghardt, G.M. and Hess, E.H. (1966). Food imprinting in the

snapping turtle, Chelydra serpentina. Science. 151, 108 - 109.

Burton, M. (1962). Systematic Dictionary of Mammals of the World.

London: Museum Press.

Butler, K. (1973). Predatory behavior in laboratory mice: Sex and

strain comparisons. J. Comp. Physiol. Psychol. 85, 243 - 249.

Bygott, J.D. (1972). Cannibalism among wild chimpanzees. Nature.

238, 410 - 411.

Campbell, B.A. and Mabry, P.D. (1972). Ontogeny of behavioral arousal:

A comparative study. J. Comp. Physiol. Psychol. 81, 371 - 379.

Capretta, P.J., Moore, M.J. and Rossiter, T.R. (1973). Establishment

and modification of food and taste preferences: Effects of

experience. J. Genetic Psychol. 89, 27 - 46.

Carter, C.S. (1972). Sexual and social behaviors in anosmic female

golden hamsters (Mesocricetus auratus). Amer. Zool. 12, 658.

Carter, C.S. and Schein, M.W. (1971). Sexual receptivity and

exhaustion in the female golden hamster. Hormones Behav.

2, 191 - 200.

Chiszar, D. and Windell, J.T. (1973). Predation by Bluegill Sunfish

(Lepomis Macrochirus Rafinesque) upon mealworm larvae (Tenebrio

Molitor). Anim. Behav. 21, 536 - 543.

Clark, L.D. (1962a). Experimental studies of the behavior of an

aggressive predatory mouse, Onychomys Leucogaster. In E.L.Bliss

(ed.), Roots of Behavior. New York : Hafner.

Clark, L.D. (1962b). A comparative view of aggressive behavior.

Amer. J. Psychiatry. 119, 336 - 341.

Cloudsley-Thompson, J.L. (1965). Animal Conflict and Adaption.

London: G.T. Foulis.

Crowcroft, P. (1966). Mice all over. London: G.T.Foulis.

Cullen, E. (1957). Adaptations in the Kittiwake to cliff-nesting.

Ibis. 99, 275 - 302.

Deese, J. and Hulse, S.H. (1967). The Psychology of Learning.

London: McGraw-Hill.

Denenberg, V.H., ed. (1972). Readings in the Development of Behavior.

Stamford, Conn: Sinaner Assoc.

Denenberg, V.H., Paschke, R.E. and Zarrow, M.X. (1968). Killing

of mice by rats prevented by the early interaction between

the two species. Psychon. Sci. 11, 39.

Denny, M.R. and Ratner, S.C. (1970). Comparative Psychology.

Homewood, Ill.: Dorsey.

DeSisto, M.J. and Huston, J.P. (1970). Effect of territory on frog

killing by rats. J. Gen. Psychol. 83, 179 - 184.

DeSisto, M.J. and Huston, J.P. (1971). Aggression and reward from

stimulating common sites in the posterior lateral hypothalamus

of rats. Comm. Behav. Biol. 6, 295 - 306.

Deutsch, J.A. (1971). Appetitive motivation. In J.L. McGaugh (ed.),

Psychobiology: Behavior From a Biological Perspective.

London: Academic Press.

Devor, M. and Murphy, M.R. (1972). Social agnosia produced by

peripheral olfactory blockage in hamsters. Amer. Zool. 12, 653.

Devor, M. and Murphy, M.R. (1973). The effect of peripheral olfactory

blockage on the social behavior of the male golden hamster.

Behav. Biol. 9, 31 - 42.

Dewsbury, D.A. and Rethlingshafer, D.A. eds. (1973) Comparative Psy-

chology: A Modern Survey. London, McGraw-Hill.

Didiergeorges, F. and Karli, P. (1967). Hormones seroides et

maturation d'un comportement d'agression interspecifique du

rat. Compt. Rend. Soc. Biol. 161, 179.

Dieterlen, F. (1959). Das Verhalten des syrischen Goldhamsters

(Mesocricetus auratus). Z. Tierpsychol. 16, 47 - 103.

Dimond, S.J. (1970). The Social Behaviour of Animals. London:

B.T. Batsford Ltd.

Doty, R.L., Carter, C.S. and Clemens, L.G. (1971). Olfactory control of sexual behavior in the male and early-androgenized female hamster. Hormones Behav. 2, 325 - 335.

Douglass, R.J., Isaacson, R.L. and Moss, R.L. (1969). Olfactory lesions, emotionality and activity. Physiol. Behav. 4, 379 - 381.

Drickamer, L.C. and Vandenberg, J.G. (1973). Predictors of social dominance in the adult female golden hamster (Mesocricetus auratus). Anim. Behav. 21, 564 - 570.

Drickamer, L.C., Vandenberg, J.G. and Colby, D.R. (1973). Predictors of social dominance in the male golden hamster (Mesocricetus auratus). Anim. Behav. 21, 557 - 563.

Eaton, R.L. (1970). The predatory sequence with emphasis on killing behaviour and its ontogeny in the cheetah (Acinonyx jubatus Schreber). Z. Tierpsychol. 27, 492 - 504.

Eckman, S.E. and Carter, C.S. (1971). Stimulation capable of abbreviating estrus in the female golden hamster. Amer. Zool. 11, 626 - 627.

Eibl-Eibesfeldt, I. (1952). Nahrwngserwerb und Beuteschema der Erdkrote (Bufo bufo L). Behaviour. 4, 1 - 35.

Eibl-Eibesfeldt, I. (1958). Das Verhalten der Nagetiere. Handbook Zool. Berl., 8(10), No. 6, 1 - 88.

Eibl-Eibesfeldt, I. (1961). The interaction of unlearned patterns and learning in mammals. In J. Delafresnaye (ed.), Brain Mechanisms and Learning. Oxford: Blackwell Scientific Publications.

Eibl-Eibesfeldt, I. (1963). Angeborenes und Erworbenes im Verhalten

einigerSäuger. Z. Tierpsychol. 20, 705 - 754.

Eibl-Eibesfeldt, I. (1970). Ethology: The Biology of Behavior.

London: Holt, Rinehart and Winston.

Eichelman, B., Dejong, W. and Williams, R.B. (1973). Aggressive

behavior in hypertensive and normotensive rat strains.

Physiol. Behav. 10, 301 - 304.

Eisenberg, J.F. and Gould, E. (1966). The behavior of Solenodon

paradoxus in captivity with comments on the behavior of other

insectivora. Zoologica. 51, 49 - 58.

Eisenberg, J.F. and Leyhausen, P. (1972). The phylogenesis of

predatory behaviour in mammals. Z. Tierpsychol. 30, 59 - 93.

Eisner, T. and Meinwald, J. (1966). Defensive secretion of anthropods.

Science. 153, 1341 - 1350.

Eloff, F.C. (1964). On the predatory habits of lions and hyaenas.

Koedoe. 7, 105 - 112.

Endroczi, E., Lissak, K. and Teledgy, G. (1958). Influence of

sexual and adrenocortical hormones on the maternal aggressivity.

Acta Physiologica. 14, 353 - 357.

Estes, R.D. and Goddard, J. (1967). Prey selection and hunting

behavior of the African wild dog. J. Wildlife Mang. 31, 52 - 70.

Etkin, W. (1964). Co-operation and competition in social behavior.

In W. Etkin (ed.), Social Behavior and Organization among

Vertebrates. Chicago: University of Chicago Press.

Etienee, A. and Howland, H. (1964). Elicitation of strikes of

predatory insects by projected images and light spots.

Experientia. 20, 152.

Ewer, R.F.(1963). The behaviour of the meerkat, Suricata suricatta

(schreber). Z. Tierpsychol. 20, 570 - 607.

Ewer, R.F. (1968a). Ethology of Mammals. London: Logos Press Ltd.

Ewer, R.F. (1968b). A preliminary survey of the behaviour in

captivity of the dasyurid marsupial, Sminthopsis crassicaudata

(Gould). Z. Tierpsychol. 25, 319 - 365.

Ewer, R.F. (1969). Some observations on the killing and eating of

prey by two dasyurid marsupials: The Mulgara, Dasycercus

cristicauda, and the Tasmanian devil, Sarcophilus harrisi.

Z. Tierpsychol. 26, 23 - 38.

Ewer, R.F. (1971). The biology and behaviour of a free-living

population of black rats, (Rattus rattus). Anim. Behav. Mono.

4, 125 - 174.

Ewer, R.F. (1973). The Carnivores. London: Weidenfeld and Nicholson.

Ewert, J.P. (1970). Neural mechanisms of prey-catching and avoidance

behavior in the toad (Bufo bufo, L). Brain Behav. Evol. 3,

36 - 56.

Flandera, V. and Novakova, V. (1971). The development of interspecies

aggression of rats towards mice during lactation. Physiol. Behav.

6, 161 - 164.

Flynn, J.P. (1967). The neural basis of aggression in cats. In

    D.C.Glass (ed.), Neurophysiology and Emotion. New York:

    Rockefeller University Press and Russell Sage Foundation.

Flynn, J.P., Venegas, H., Foote, W. and Edwards, S. (1970).

    Neural mechanisms involved in a cat's attack on a rat. In

    R. Whalen, R.F. Thompson, M. Verzeano and N. Weinberger (eds.),

    The Neural Control of Behavior. New York: Academic Press.

Fox, M.W. (1969). Ontogeny of prey-killing behavior in Canidae.

    Behaviour, 35, 259 - 272.

Fox, M.W. (1971). Behaviour of Wolves, Dogs and Related Canids.

    London: Jonathan Cape.

Foxx, R.M. (1972). Attack preferences of the red-bellied piranha,

    Serrasalmus nattereri. Anim. Behav. 20, 280 - 283.

Fuller, J.L. (1967). Effects of the albino gene upon behavior of

    mice. Anim. Behav. 15, 467 - 470.

Galef, B.G. (1970). Aggression and timidity: Responses to novelty

    in feral norway rats. J. Comp. Physiol. Psychol. 70, 370 - 381.

Galef, B.G. and Henderson, P.W. (1972). Mother's milk: A determinant

    of the feeding preferences of weaning rat pups. J. Comp.

    Physiol. Psychol. 78, 213 - 219.

Galef, Jr., B.G. and Sherry, D.F. (1973). Mother's milk: A medium

    of transmission for cues reflecting the flavor of mother's

    diet. J. Comp. Physiol. Psychol. 83, 374 - 378.

Gandelman, R. (1972). Induction of pup killing in female mice by androgenization. Physiol. Behav. 9, 101 - 102.

Gandelman, R. (1973). The development of cannibalism in male Rockland - Swiss mice and the influence of olfactory bulb removal. Devel. Psychobiology. 6, 159 - 164.

Gandelman, R., Zarrow, M. and Denenberg, V.H. (1971). Stimulus control of cannibalism and maternal behavior in anosmic mice. Physiol. Behav. 7, 583 - 586.

Gandelman, R., Zarrow, M.X., Denenberg, V.H. and Myers, M. (1971). Olfactory bulb removal eliminates maternal behavior in the mouse. Science. 171, 210 - 211.

Garattini, S. and Sigg, E.B. eds.(1969). Aggressive Behaviour. Amsterdam: Excerpta Medica Foundation.

Gardner, B.T. (1964). Hunger and sequential responses in the hunting behavior of salticid spiders. J. Comp. Physiol. Psychol. 58, 167 - 173.

Goodall, J. (1963). Feeding behaviour of wild chimpanzees: A preliminary report. Symp. Zool. Soc. Lond. 10, 39.

Gossow, V.H. (1970). Vergleichende Verhaltensstudien an Marderatigen. I. Über LäutauBerungen und zum Beuteverhalten. Z. Tierpsychol. 27, 405 - 480.

Grant, E.C., Mackintosh, J.H. and Lerwill, C.J. (1970). The effect of a visual stimulus on the agonistic behaviour of the golden hamster. Z. Tierpsychol. 27, 71 - 77.

Gray, J. (1971). The Psychology of Fear and Stress. London:
Weidenfeld and Nicholson.

Griffen, D.R., Webster, F.A. and Michael, C.R. (1960). The
echolocation of flying insects by bats. Anim. Behav. 8,
141 - 154.

Hafez, E.S.E., ed. (1962). The Behavior of Domestic Animals.
London: Bailliere, Tindell & Cox.

Hall, K.R.L. and Schaller, G.B. (1964). Tool using behavior of
.the California sea otter. J. Mammalogy. 45, 287 - 298.

Hammer, L.R. (1972). Further hoarding preferences in hamsters.
Psychon. Sci. 26, 139 - 140.

Harrison - Matthews, L. (1971) The Life of Mammals. Vol. 2.
London: Weidenfeld and Nicholson.

Heimstra, N.W. (1965). A further investigation of the development
of mouse killing in rats. Psychon. Sci. 2, 179 - 180.

Heimstra, N.W. and Newton, G. (1961). Effects of prior food
competition on the rat's killing response to the white mouse.
Behaviour. 17, 95 - 102.

Hemmer, H. (1968). Zur Kenntnis des Beutefangverhaltens verschiedener
Rodentia, besonders des Hamsters (Cricetus cricetus L). Zool.
Beiträge. 14, 471 - 488.

Hess, E.H. (1964). Imprinting in birds. Science. 146, 1123 - 1139.

Hinde, R.A. (1954). Factors governing the changes in strength of

a partially inborn response, as shown by the mobbing behaviour

of the chaffinch (Fringilla coelebs). I. The nature of the

response and an examination of its course. Proc. Roy. Soc. Lond.

(B). 142, 306 - 331.

Hinde, R.A. (1970). Animal Behaviour: A Synthesis of Ethology and

Comparative Psychology. 2nd edition. London: McGraw-Hill.

Hinde, R.A. and Tinbergen, N. (1958). The comparative study of

.species-specific behavior. In A. Roe and G.G. Simpson (eds).

Behavior and Evolution. New Haven: Yale Univ. Press.

Hirsch, J., Lindley, R.H. and Tolman, E.C. (1955). An experimental

test of an alleged innate sign stimulus. J. Comp. Physiol.

Psychol. 48, 278 - 280.

Hodos, W. and Campbell, C.B.G. (1969). Scala naturae: Why there is

no theory in comparative psychology. Psychol. Rev. 76, 337 - 350.

Hogan, J.A. (1973a). Development of food recognition in young chicks.

II. Learned associations over long delays. J. Comp. Physiol.

Psychol. 83, 367 - 373.

Hogan, J.A. (1973b). How young chicks learn to recognize food. In

R.A. Hinde and J. Stevenson-Hinde (eds.), Constraints on

Learning. London: Academic Press.

Holling, C.S. (1959). The components of predation as revealed by

a study of small mammal predation of the European pine sawfly.

Canadian Ent. 91, 293 - 320.

Hoogland, R., Morris, D. and Tinbergin, N. (1957). The spines of

the sticklebacks (Gasterosteus and Pygosteus) as a means of

defence against predators. Behaviour. 10, 205 - 236.

Horner, B.E., Taylor, J. and Padykula, H.A. (1965). Food habits

and gastric morphology of the grasshopper mouse. J. Mammology.

45, 513 - 536.

Horovitz, A.P., Piala, J.J., High, J.P., Burke, J.C. and Leaf, R.C.

(1966). Effects of drugs on mouse-killing (muricide) test and

its relationship to amygdaloid function. Int. J. Neuropharmac.

5, 405 - 411.

Horowitz, Z.P., Ragozzind, P.W. and Leaf, R.C. (1965). Selective

block of rat - mouse killing by antidepressants. Life Sci. 4,

1909 - 1912.

Hunter - Jones, P. (1961). Rearing and breeding locusts in the

laboratory. Publication of the Anti - Locust Research Centre,

London.

Huston, J.P. and DeSisto, M.J. (1971). Interspecies aggression

during fixed-ratio hypothalamic self-stimulation in rats.

Physiol. Behav.7, 353 - 357.

Hutchinson, R.R. and Renfrew, J.W. (1966). Stalking attack and

eating behaviors elicited from the same site in the hypothal-

amus. J. Comp. Physiol. Psychol. 61, 360 - 367.

Ingle, D. (1973a). Size preferences for prey-catching in frogs:

Relationship to motivational state. Behav. Biol. 9, 485 - 491.

Ingle, D. (1973b). Reduction of habituation of prey-catching activity by alcohol intoxication in the frog. Behav. Biol. 8, 123 - 129.

Ingle, D. (1973c). Selective choice between double prey objects by frogs. Brain Behav. Evol. 7, 127 - 142.

Jacobs, D.L. (1945). Food habits of the golden hamster. J. Mammalogy. 26, 199.

Johnson, R.N. (1972). Aggression in Man and Animals. London: W.B. Saunders Co.

Johnson, R.N., DeSisto, M.J. and Koenig, A.B. (1970). Social experience and interspecies aggression in rats. Proceedings of the Annual Convention of the American Psychological Assoc. 5, 231 - 232.

Johnson, R.N., DeSisto, M.J. and Koenig, A.B. (1972). Social and developmental experience and interspecific aggression in rats. J. Comp. Physiol. Psychol. 79, 237 - 242.

Johnson, W.A. and Tiefer, L. (1972). Sexual preferences in neonatally castrated male golden hamsters. Physiol. Behav. 9, 213 - 217.

Johnston, R.E. (1972). Sex pheromones of the golden hamster. Amer. Zool. 12, 662.

Johnston, R.E. (1974). Sexual attraction function of golden hamster vignal secretion. Behav. Biol. 12, 111 - 117

Karli, P. (1966). The Norway rat's killing response to the white mouse: An experimental analysis. Behavior. 10, 81 - 101.

Karli, P. (1958). Hormones steroides et comportement d'agression interspecifique rat - souris. J. Physiol. Gen. Path. 50, 346 - 357.

Karli, P. (1961). Role des afferences sensorielles dans le declenchement du comportement d'aggression interspecifique rat-souris. Compte Rendu des Seances de la Societe de Biologie. 155, 644 - 646.

Karli, P., Vergnes, M. and Didiergeorges, F. (1969). Rat-mouse interspecific aggressive behaviour and its manipulation by brain ablation and by brain stimulation. In S. Garattini and E.B. Sigg (eds.), Aggressive Behaviour. Amsterdam: Excerpta Medica Foundation.

Kilbey, M.M., Moore, J.M. and Hall, M. (1973). Delta - 9 tetrahydrocannabinol induced inhibition of predatory aggression in the rat. Psychopharmacologia. 31, 157 - 166

Kilby, M.M., Moore, J.W. and Harris, R.T. (1973). Delta - 9 tetrahydrocannabinol on appetitive and aggressive rewarded maze performance. Physiol. Psychol. 1, 174 - 176.

King, M.B. and Hoebel, B.G. (1968). Killing elicited by brain stimulation in the rat. Comm. Behav. Biol. 2, 173 - 177.

Klopfer, P.H. (1962). Behavioral Aspects of Ecology. Englewood Cliffs, N.J. Prentice-Hall, Inc.

Klugh, H.E. (1970). Statistics: The Essentials for Research.
London: Wiley.

Korn, J.H. and Moyer, K.E. (1968). Behavioral effects of isolation
in the rat; The role of sex and time of isolation. J. Genet.
Psychol. 113, 263 - 273.

Krehbiel, R.H. (1952). Mating of the golden hamster during pregnancy
Anatomical Rec. 113, 117 - 121.

Kreiskott, H. (1969). Some comments on the killing response of the
rat. In S. Garattini and E.B. Sigg (eds.), Aggressive Behaviour
Amsterdam: Excerpta Medica Foundation.

Kruuk, H. (1969). Interactions between populations of spotted
hyaenas and their prey species. In A. Watson (ed.), Animal
Populations in Relation to Food Resources. Oxford : Blackwell.

Kruuk, H. (1972a). The Spotted Hyena: A Study of Predation and Social
Behaviour. Chicago: Univ. Chicago Press.

Kruuk, H. (1972b). Surplus killing by carnivores. J. Zool. 166,
233 - 244.

Kruuk, H. and Turner, M. (1967). Comparative notes on predation by
lion, leopard, cheetah and wild dog in the Serengeti area, East
Africa. Mammalia. 31, 1 - 27.

Kuhme, W. (1965). Communal food distribution and division of labor
in African hunting dogs. Nature. 209, 1257 - 1258.

Kulkarni, A.S. (1968a). Satiation of instinctive mouse killing by
rats. Psychol. Rec. 18, 385 - 388.

Kulkarni, A.S. (1968b). Muricidal block produced by 5-hydroxtryptophan and various drugs. Life Sci. 7, 125 - 128.

Kumadaki, N., Hitomi, M. and Kumada, S. (1967). Effect of psycho-therapeutic drugs on hyperemotionality of rats in which the olfactory bulb was removed. Jap. J. Pharm. 17, 659 - 667.

Kuo, Z.Y. (1930). The genesis of the cat's responses to the rat. J. Comp. Psychol. 11, 1 - 35.

Kuo, Z.Y. (1938). Further study on the behavior of the cat towards the rat. J. Comp. Physiol. Psychol. 25, 1 - 8.

Kuo, Z.Y. (1960). Studies on the basic factors in animal fighting. VII. Inter-species coexistence in mammals. J. Genet. Psychol. 97, 211 - 225.

Kuo, Z.Y. (1967). The Dynamics of Behavioral Development: An Epigenetic View. New York: Random House.

Lagerspetz, K. (1964). Studies on the aggressive behaviour of mice. Suomalaisen Tiedeakatemian Toimituksia. Ann. Acad. Scient.Fenn. 131, 1 - 131.

Lagerspetz, K. and Heino, T. (1970). Changes in social reactions result-ing from early experience with another species. Psychol. Rep. 27, 255 - 262.

Landry, S.O. (1970). The rodentia as omnivores. Quart. Rev. Biol. 45, 351 - 372.

Lawlor, M. (1963). Social dominance in the golden hamster. Bull. Brit. Psychol. Soc. 16, 1 - 14.

Leonard, C. (1972). Effects of neonatal (Day 10) olfactory bulb
lesions on social behavior of female golden hamsters.
(Mesocricetus auratus). J. Comp. Physiol. Psychol. 80,
208 - 215.

Lerwill, C.J. (1968). Agonistic Behaviour and Social Dominance in
the Golden Hamster. M.Sc. Thesis. Univ. of Wales.

Lerwill, C.J. and Makings, P. (1971). The agonistic behaviour of
the golden hamster, Mesocricetus auratus (Waterhouse). Anim.
Behav. 19, 714 - 721.

Levison, P.K. and Flynn, J.P. (1965). The objects attacked by cats
during stimulation of the hypothalamus. Anim. Behav. 13,
217 - 220.

Leyhausen, P. (1956). Verhaltensstudien an Katzen. Z. Tierpsychol.
Beiheft 2, 1 - 120.

Leyhausen, P. (1965). Über die Funktion der relativen Stimmung-
shierarchie. Z. Tierpsychol. 22, 412 - 494.

Leyhausen, P. (1973). On the function of the relative hierarchy of
moods (as exemplified by the phylogenetic and ontogenetic
development of prey-catching in carnivores). In K. Lorenz and
P. Leyhausen (eds.), Motivation of Human and Animal Behavior.
London: Van Nostrand Reinhold.

Lisk, R.D., Zeiss, J. and Ciaccio, L.A. (1971). The influence of
olfaction on sexual behavior in the male golden hamster.
J. Exper. Zool. 181, 69 - 78.

Lockard, R.B. (1971). Reflections on the fall of comparative
      psychology: Is there a message for us all ? Amer. Psychol. 26,
      168 - 179.

Lonowski, D.J., Levitt, R.A. and Larson, S.D. (1973). Mouse killing
      or carrying by male and female Long-evans hooded rats. Bull.
      Psychon. Soc. 1, 349 - 351.

Loop, M.S. and Bailey, L.G. (1972). The effect of relative prey
      size on the injestion behavior of rodent - eating snakes.
      Psychon. Sci. 28, 167 - 169.

Lorenz, K. (1965). Evolution and Modification of Behaviour.
      Chicago: Univ. Chicago Press.

Lorenz, K. (1966). On Aggression. New York: Harcourt Brace, and
      World.

MacDonnell, M. and Flynn, J.P. (1966). Sensory control of
      hypothalamic attack. Anim. Behav. 14, 399 - 405.

Maier, R.A. and Maier, B.M. (1970). Comparative Animal Behavior.
      Belmont, Calif. Brooks - Cole.

Malick, J.B. (1970). A behavioral comparison of three lesion-induced
      models of aggression in the rat. Physiol. Behav. 5, 679 - 681.

Manning, A. (1967). An Introduction to Animal Behaviour. 1st edition.
      London: E. Arnold, Ltd.

Markl, H.C. (1972). Aggression und beuteverhalten bei Piranhas
      (Serrasalminae, Characidae). Z. Tierpsychol. 30, 190 - 216.

Marler, P. and Hamilton, W.J. (1966). Mechanisms of Animal Behavior. London: Wiley.

McDonough Jr., J.H., Manning, F.J. and Elsmore, T.F. (1972). Reduction of predatory aggression of rats following administration of delta-9 tetrahydrocannabinol. Life Sci. 11, 103 - 111.

McGaugh, J.L., Jennings, R.D. and Thompson, C.W. (1962). Effect of distribution of practice on the maze learning of the descendants of the Tryon maze bright and maze dull strains. Psychol. Rep. 10, 147 - 150.

Melzack, R., Penick, E. and Beckett, A. (1959). The problem of 'innate fear' of the hawk shape: An experimental study with mallard ducks. J. Comp. Physiol. Psychol. 52, 694 - 698.

Meyer, M.E. and Frank, L.H. (1970). Food imprinting in the domestic chick: A reconsideration. Psychon. Sci. 19, 43 - 45.

Miczek, K.A. and Grossman, S.P. (1972). Effects of septal lesions on inter- and intraspecies aggression in rats. J. Comp. Physiol. Psychol. 79, 37 - 45.

Miley, W.M. and Baenninger, R. (1972). Inhibition and facilitation of interspecies aggression in septal lesioned rats. Physiol. Behav. 9, 694 - 698.

Miller, C.R. (1972). Sexual satiety in the male golden hamster (Mesocricetus auratus). Dissertation Abstracts. 32, 6082.

Moltz, H. (1965). Contempory instinct theory and the fixed action pattern. Psychol. Rev. 72, 27 - 47.

Moltz, H. (1971). Ontogeny of mammalian maternal behavior. In
H. Moltz (ed.), The Ontogeny of Vertebrate Behavior. London:
Academic Press.

Morris, D. (1965). The Mammals: A Guide to the Living Species.
London: Hodder and Stoughton.

Moyer, K.E. (1968). Kinds of aggression and their physiological
basis. Comm. Behav. Biol. 2, 65 - 87.

Moyer, K.E. (1971). A preliminary physiological model of aggressive
behavior. In B.E. Eleftheriou and J.P.Scott (eds.), The
Physiology of Aggression and Defeat. London: Plenum Press.

Mueller, H.C. (1973). The relationship of hunger to predatory
behavior in hawks (Falco Sparuerius and Buteo Platypterus).
Anim. Behav. 21, 513 - 520.

Mueller, H.C. and Berger, D.D. (1970). Prey-preferences in the
sharp - shinned hawk: The roles of sex, experience, and
motivation. Auk. 87, 452 - 457.

Murphy, M.R. (1970). Territorial behavior of the caged golden
hamster. Proceedings 78th Ann. Convent. A.P.A. 237 - 238.

Murphy, M.R. (1971). Natural history of the Syrian golden hamster -
a reconnaissance expedition. Amer. Zool. 11, 632.

Murphy, M.R. and Schneider, G.E. (1970). Olfactory bulb removal
eliminates mating behavior in the male golden hamster. Science.
167, 302 - 304.

Myer, J.S. (1964). Stimulus control of mouse-killing rats.

J. Comp. Physiol. Psychol. 58, 112 - 117.

Myer, J.S. (1966). Punishment of instinctive behavior: Suppression

of mouse killing by rats. Psychon. Sci. 4, 385 - 386.

Myer, J.S. (1967). Prior killing experience and the suppressive

effects of punishment on the killing of mice by rats. Anim.

Behav. 15, 59 - 61.

Myer, J.S. (1968). Associative and temporal determinants of

. facilitation and inhibition of attack by pain. J. Comp.

Physiol. Psychol. 66, 17 - 21.

Myer, J.S. (1969). Early experience and the development of mouse

killing by rats. J. Comp. Physiol. Psychol. 67, 46 - 49.

Myer, J.S. (1971). Experience and the stability of mouse killing

by rats. J. Comp. Physiol. Psychol. 75, 264 - 268.

Myer, J.S. and Baenninger, R. (1966). Some effects of punishment

and stress on mouse killing by rats. J. Comp. Physiol. Psychol.

62, 292 - 297.

Myer, J.S. and White, R.T. (1965). Aggressive motivation in the

rat. Anim. Behav. 13, 430 - 433.

Newton, G. and Levine, S., eds. (1968). Early Experience and Behavior.

Springfield, Ill: C.C. Thomas.

Noble, R.G. (1973a). Facilitation of the lordosis response of the

female hamster (Mesocricetus auratus). Physiol. Behav. 10,

663 - 666.

Noble, R.G. (1973b). Sexual arousal of the female hamster.
Physiol. Behav. 10, 973 - 975.

Noirot, E. (1969). Changes in responsiveness to young in the adult
mouse. V. Priming. Anim. Behav. 17, 542 - 546.

Noirot, E. (1972). The onset of maternal behavior in rats,
hamsters, and mice: A selective review. In D.S. Lehrman,
R.A. Hinde, E. Shaw (eds.), Advances in the Study of Behavior.
Vol. 4. London: Academic Press.

Noirot, E. and Richards, M.P.M. (1966). Maternal behavior in
virgin female golden hamsters: Changes consequent upon initial
contact with pups. Anim. Behav. 14, 7 - 10.

Nucci, P. and Beach, F.A. (1971). Effects of prenatal androgen
treatment on mating behavior in female hamsters. J. Endrocrin.
88, 1514 - 1515.

Orians, G.H. (1969). Age and hunting success in the brown pelican
(Pdecanus occidentalis). Anim. Behav. 17, 316 - 319.

Panksepp, J. (1971a). Aggression elicited by electrical stimulation
of the hypothalamus in albino rats. Physiol. Behav. 6, 321 - 329.

Panksepp, J. (1971b). Effects of hypothalamic lesions on mouse-killing
and shock-induced fighting in rats. Physiol. Behav. 6,
311 - 316.

Panksepp, J. (1971c). Drugs and stimulus bound attack. Physiol. Behav.
6, 317 - 320.

Panksepp, J. and Trowill, J. (1969). Electrically induced affective attack from the hypothalamus of the albino rat. Psychon. Sci. 16, 118 - 119.

Paul, L. (1972). Predatory attack by rats: Its relationship to feeding and type of prey. J. Comp. Physiol. Psych. 78, 69 - 76.

Paul, L., Miley, W.M. and Baenninger, R. (1971). Mouse killing by rats: Roles of hunger and thirst in its initiation and mainten-. ance. J. Comp. Physiol. Psychol. 76, 242 - 249.

Paul, L., Miley, W.M. and Mazzagatti, N. (1973). The social facilitation and inhibition of hunger-induced killing by rats. J. Comp. Physiol. Psychol. 84, 162 - 168.

Paul, L. and Posner, I. (1973). Predation and Feeding: Comparisons of feeding behavior of killer and nonkiller rats. J. Comp. Physiol. Psych. 84, 258 - 264.

Payne, A.P. (1973). A comparison of the aggressive behaviour of isolated intact and castrated male golden hamsters towards intruders introduced into the home cage. Physiol. Behav. 10, 629 - 631.

Payne, A.P. and Swanson, H.H. (1970). Agonistic behaviour between pairs of hamsters of the same and opposite sex in a neutral observation area. Behaviour. 36, 259 - 269.

Payne, A.P. and Swanson, H.H. (1972a). The effect of sex hormones on the agonistic behavior of the male golden hamster. (Mesocricetus auratus Waterhouse). Physiol. Behav. 8, 687 - 691.

Payne, A.P. and Swanson, H.H. (1972b). The effect of sex hormones on
the aggressive behavior of the female golden hamster (Mesocricetus
auratus Waterhouse). Anim. Behav. 20, 782 - 787.

Payne, A.P. and Swanson, H.H. (1972c). Neonatal androgenization and
aggression in the male golden hamster. Nature. 239, 282 - 283.

Payne, R.S. (1961). The acoustical localization of prey in the barn
owl (Tyto albo). Amer. Zool. 1, 379.

Pion, L.V. (1969). Early experience, social contact and the incidence
of mouse killing behavior in Norway rats. Amer. Zool. 9, 10.

Polsky, R.H. (1974). Effects of novel environment on predatory
behavior of golden hamsters. Percept. Motor Skills. 39, 55 - 58.

Polsky, R.H. (1975). Hunger, prey feeding, and predatory aggression.
Behav. Biol. 13, 81 - 93.

Poole, T.B. (1966). Aggressive play in polecats. Symp. Zool. Soc.
Lond. 18, 23 - 44.

Powers, J.B. and Winans, S.S. (1973). Sexual behavior in peripherally
anosmic male hamsters. Physiol. Behav. 10, 361 - 368.

Purohit, K.G. (1967). The Great Indian desert: Perspectives in
the ecology and physiology of small desert mammals. Mammalia.
31, 28 - 49.

Rabinowitch, V. (1968). The role of experience in the development
of food preferences in gull chicks. Anim. Behav. 16, 425 - 428.

Rasa, O.A.E. (1973). Prey capture, feeding techniques, and their ontogeny in the African Dwarf mongoose, Helogale undulata rufula. Z. Tierpsychol. 32, 449 - 488.

Reed, C.A. and Reed, R. (1946). The copulatory behavior of the golden hamster. J. Comp. Psychol. 39, 7 - 12.

Relvis, R. Moyer, K.E. (1969). Maternal aggression: A failure to replicate. Psychon. Sci. 16, 136 - 136.

Richards, M.P.M. (1967). Maternal behaviour in rodents and lagomorphs. In A. McLaren (ed.), Advances in Reproductive Physiology. Vol.2. New York: Academic Press.

Rilling, S., Mittelstaedt, H. and Roeder, K.D. (1959). Prey recognition in the praying mantis. Behaviour. 14, 164 - 184.

Roberts, W.W. and Berquist, E.H. (1968). Attack elicited by hypothalamic stimulation in cats raised in social isolation. J. Comp. Physiol. Psychol. 66, 590 - 595.

Roberts, W.W. and Kiss, H.O. (1964). Motivational properties of hypothalamic aggression in cats. J. Comp. Physiol. Psychol. 58, 187 - 193.

Roberts, W.W., Steinberg, M.L. and Means, L.W. (1967). Hypothalamic mechanisms for sexual and other motivational behaviors in the opossum. Didilphis Virginiana. J. Comp. Physiol. Psychol. 64, 1 - 15.

Rood, J.P. (1958). Habits of the short-tailed shrew in captivity. J. Mammalogy. 39, 499 - 507.

Rosenberg, K.M, Denenberg, V.H., Zarrow, M.X. and Frank, B.L. (1971).
Effects of neonatal castration and testosterone on the rat's
pup killing behavior and activity. Physiol. Behav. 7, 363 - 368.

Ross, E.S. (1965). Asian insects in disguise. Nat. Geog. 128,
432 - 439.

Rozin, P. and Kalat, J.W. (1971). Specific hungers and poison
avoidance as adaptive specializations of learning. Psychol.
Rev. 78, 459 - 486.

Ruffèr, D.G. (1965). Sexual behavior of the Northern grasshopper
mouse (Onychomys leucogaster). Anim. Behav. 13, 447 - 451.

Rundquist, E.A. (1933). Spontaneous activity and maze learning.
J. Comp. Psychol. 16, 415 - 438.

Sachs, L. (1952). Polyploid evolution and mammalian chromosomes.
Heredity. 6, 357 - 364.

Scelfo, L.M. and Hammer, L.R. (1969). Stimulus preferences in
hoarding. Psychon. Sci. 17, 155 - 156.

Schaller, G.B. (1967). The Deer and the Tiger. Chicago: Univ.
Chicago Press.

Schaller, G.B. (1972). The Serengeti Lion: A Study of Predator-
Prey Relations. Chicago: Univ. Chicago Press.

Schenkel, R. (1966). Play, exploration and territory in the wild
lion. In P.A. Jewell and C. Loizos (eds.), Play, Exploration
and Territory in Mammals. London: Academic Press.

Schnierla, T.C. (1959). An evolutionary and developmental theory
of biphasic processes underlying approach and withdrawal.
In M.R. Jones (ed.), Nebraska Symposium on Motivation.
Lincoln: Univ. Nebraska Press.

Scott, J.P. (1958). Animal Behavior. Chicago: Univ. Chicago Press.

Scott, J.P. (1964). The effects of early experience on social
behavior and organization. In Social Behavior and Organization
among Vertebrates. W. Etkin (ed.). Chicago: Univ. Chicago Press.

Scott, J.P.(1966). Agnostic Behavior of Mice and Rats: A review.
Amer. Zool. 6, 683 - 701.

Scott, J.P. (1973). Hostility and aggression. In B.B.Wolman (ed).,
Handbook of General Psychology. Englewood Cliffs, N.J. Prentice
Hall.

Scott J.P. and Fredericson, E. (1951). The causes of fighting in
mice and rats. Physiol. Zool. 24, 273 - 309.

Scott, E.M. and Quint, E. (1946). Self-selection of diet. III.
Appetites for B vitamins. J. Nutrition. 32, 285 - 291.

Scott, J.P. and Bronson, F.H. (1964). Experimental exploration of
the et-epimeletic or care - soliciting behavioral system. In
P.H. Leiderman and D. Shapiro (eds.), Psychobiological Approaches
to Social Behavior. London: Tavistock Publications.

Seago, J.B., Ludvigson, H.W. and Remlez, N.R. (1970). Effects of
anosmia on apparent double alternation in the rat. J. Comp.
Physiol. Psychol. 71, 433 - 442.

Shettleworth, S. (1973). Food reinforcement and the organization
of behavior in golden hamsters. In R.A. Hinde and J. Stevenson-
Hinde (eds.), Constraints on Learning: Limitations and Predis-
positions. London: Academic Press.

Sieck, M.H. (1973). Selective olfactory systems lesions in appetitive
and aversive behavior. Physiol. Behav. 10, 731 - 739.

Siegel, S. (1956). Nonparametric Statistics for the Behavioral
Sciences. London: McGraw - Hill.

Sluckin, W. (1970). Early Learning in Man and Animal. London:
Allen and Unwin.

Sluckin, W. ed., (1971). Early Learning and Early Experience.
Middlesex. Penguin Books.

Smith, S.M. (1973). A study of prey attack in young loggerhead
shrikes, Lannius Ludovicianus, L. Behaviour. 34, 113 - 141.

Smith, D.E., King, M.B. and Hoebel, B.G. (1970). Lateral hypothalamic
control of killing: Evidence for a cholinoceptive mechanism.
Science. 167, 900 - 901.

Smith, W.J. and Ross, S. (1950). Hoarding behavior in the golden
hamster. J. Genet. Psychol. 77, 211 - 215.

Smith, W.J. and Ross, S. (1953). The role of activity in hoarding.
Anat. Rec. 117, 564.

Spector, S.A. and Hull, E.M. (1972). Anosmia and mouse killing by
rats: A nonolfactory role for the olfactory bulbs. J. Comp.
Physiol. Psychol. 80, 354 - 356.

Swanson, H.H. (1966). Sex differences in behavior of hamsters in the open field and emergence tests: Effects of pre- and post-pubertal gonadectomy. Anim. Behav. 14, 522 - 529.

Swanson, H.H. (1969). Alteration of sex-typical behaviour of hamsters in open field and emergence tests by neo-natal administration of androgen or oestrogen. Anim. Behav. 15, 209 - 216.

Swanson, H.H. (1969). Interaction of experience with adrenal and sex hormones on the behaviour of hamsters in the open field test. Anim. Behav. 17, 148 - 154.

Swanson, H.H. and Crossley, D.A. (1971). Sexual behavior in the golden hamster and its modification by neonatal administration of testosterone propionate. In M. Hamburgh and E.J.W. Barrington (eds.), Hormones in Development. New York: Appleton-Cetury-Crofts.

Teleki, G. (1973). The omnivorous chimpanzee. Sci. Amer. 228, 32 - 42.

Thomas, K. (1969). Predatory behavior in two strains of laboratory mice. Psychon. Sci. 15, 13 - 14.

Thomas, K. (1971). Predatory behavior in mice: Strain and sex comparisons. Paper presented to the Western Psychol. Assoc. Meeting. April, 1971.

Thomas, K. (1972). Selective breeding for fast and slow cricket-killing in laboratory mice. Paper presented to the Anim. Behav. Soc. June, 1972.

Thomas, K. and Fried, M. (1971). Speed of predatory attack in
Mus musculus, Peromyscus californicus, and Onychomys torridus.
Paper read to the American Society of Mammalogists. June, 1971.

Thorndike, E.L. The law of effect. In D. Bindra and J. Stewart,
eds. (1966). Motivation. Middlesex: Penguin Books.

Thorne, B.M., Aaron, M. and Latham, E.E. (1973). Effect of olfactory
bulb ablation upon emotionality and muricidal behavior in four
rat strains. J. Comp. Physiol. Psych. 84, 339 - 344.

Tiefer, L. (1970) Gonadal hormones and mating behavior in the adult
golden hamster. Hormones Behav. 1, 189 - 202.

Tiefer, L. and Johnson, W.A. (1971). Female sexual behavior in male
golden hamsters. J. Endrocrin. 51, 615 - 620.

Tinbergen, N. (1951). The Study of Instinct. Oxford: Clarendon Press

Tinbergen, N. (1953). Social Behaviour in Animals. London: Methuen.

Tinbergen, N. (1963). On the aims and methods of ethology.
Z. Tierpsychol. 20, 410 - 429.

Tobach, E. and Gold, P. (1962). Eliminative response in the albino
hamster. Nature. 196, 352 - 353

Tryon, R.C. (1942). Individual differences. In F.A. Moss (ed.),
Comparative Psychology. New York: Prentice Hall.

Tugendhat, B. (1960). The normal feeding behavior of the three-
spined stickleback (Gasterosteus aculeatus L.). Behaviour.
15, 284 - 318.

Ueki, S., Fujiwara, M. and Ogawa, N. (1972). Mouse-killing behaviour
(muricide) induced by delta - 9 tetrahydrocannabinol in the rat.
Physiol. Behav. 9, 585 - 587.

Ulrich, R.E., Wolff, P.C. and Azrin, N.H. (1964). Shock as an
elicitor of intra- and inter-species fighting behavior.
Anim. Behav. 12, 14 - 15.

Valzelli, L. (1967). Drugs and aggressiveness. Adv. Pharm. 5,
79 - 106.

Van Hemel, P. (1972). Aggression as a reinforcer: Operant
behavior in the mouse-killing rat. J. Exp. Anal. Behav. 17,
237 - 245.

Van Hemel, P.E. and Myer, J.S. (1970). Satiation of mouse killing
by rats in an operant situation. Psychon. Sci. 21, 129 - 130.

Vergnes, M. and Karli, P. (1969). Effets de la stimulation de
l'hypothalamus lateral, de l'amygdale et de l'hippocampe sur
le comportement d'agression inter specifique rat - souris.
Physiol. Behav. 4, 889 - 894.

Vergnes, M. and Karli, P. (1970). Declenchement d'un comportement
d'agression par stimulation electrique de l'hypothalamus median
chez le rat. Physiol. Behav. 5, 1427 - 1430.

Vogel, J.R. and Haubrich, D.R. (1973). Chronic administration of
electroconvulsive shock: Effects on mouse-killing activity and
brain monoamines in rats. Physiol. Behav. 11, 725 - 728.

Vogel, J.R. and Leaf, R.C. (1972). Initiation of mouse killing in
    nonkiller rats by repeated pilocarpine treatment. Physiol.
    Behav. 8, 421 - 424.

Waddell, D. (1951). Hoarding behavior in the golden hamster.
    J. Comp. Physiol. Psychol. 44, 383 - 388.

Walker, E.P. (1968). Mammals of the World. Vol. 2. Baltimore:
    John Hopkins Press.

Warren, J.M. (1965). Primate learning in comparative perspective.
    In H.F.Harlow and F. Stollnitz (eds.), Behavior of Nonhuman
    Primates. Vol. 1. London: Academic Press.

Wasman, M. and Flynn, J.P. (1962). Directed attack elicited from
    the hypothalamus. Arch. Neurol. 6, 220 - 227.

Waterhouse, G.R. (1839). Description of a new species of hamster.
    (Cricetus auratus). Proc. Lond. Zool. Soc. 7, 57 - 58.

Webster, F.A. and Griffen, D.R. (1962). The role of flight membranes
    in insect capture by bats. Anim. Behav. 10, 332 - 340.

Weisz, P.B. (1968). Elements of Zoology. London: McGraw-Hill

Welker, W.I. and King, W.A. (1962). Effects of stimulus novelty on
    gnawing and eating by rats. J. Comp. Physiol. Psychol. 55,
    838 - 842.

Whalen, R.E. and Fehr, H. (1964). The development of the mouse
    killing response in rats. Psychon. Sci. 1, 77 - 78.

Wharton, G.W. and Arlian, L.G. (1972). Predatory behavior of the mite,
    Cheyletus Averson. Anim. Behav. 20, 719 - 723.

552.

Whitney, R. (1963). Hamsters. In W. Lane-Petter (ed.), Animals for Research: Principles of Breeding and Management. London: Academic Press.

Whittaker, R.H. and Feeny, P.P. (1971). Allelochemics: Chemical interactions between species. Science. 171, 757 - 770.

Wickler, W. (1968). Mimicry in Plants and Animals. London: World Univ. Library.

Wimer, R.E., Symington,L., Farmer, H. and Schwartzkroin, P. (1968). J. Comp. Physiol. Psychol. 65, 126 - 131.

Winer, B.J. (1970). Statistical Principles in Experimental Design. London: McGraw-Hill.

Wüstehube, C. (1960). Beiträge z. Kenntnis besonders des Spiel - und Beutefangverhaltens einheimischer Musteliden. Z. Tierpsychol. 17, 579 - 613.

Wynne-Edwards, V.C. (1962). Animal Dispersion in Relation to Social Behaviour. Edinburgh: Oliver and Boyd.

Yerkes, R.W. and Bloomfield, D. (1970). Do kittens instinctively kill mice ? Psychol. Bull. 7, 253 - 263.

Young, P.T. (1948). Appetite, palatability and feeding habit: A critical review. Psychol. Bull. 45, 289 - 320.

Young, P.T. (1967). Palatability: The hedonic response to foodstuffs. In Handbook of Physiology. Vol. I. Sec. 6. Alimentary Canal. Amer. Physiological Soc.

Zim, H.S. (1951). Golden Hamsters. New York: W. Morrow.

The treatise opens with a literature review on predatory

behaviour in mammals. Areas discussed included species of investiga-

tion, methods of investigation, behavioural patterns, developmental

and motivational aspects, the effect of hormones and the stimuli

involved in the control of the response. A conclusion which emerged

was that more research was needed with species other than the albino

rat.

This conclusion served as the impetus for experimentation on

the ontogeny of predation in the golden hamster (M.a.auratus). In

total, a pilot study, which focused on the qualitative aspects of

the response, and 12 experiments were reported. The prey used through-

out were nymphs of the species Locusta migratoria. The basic method-

ology consisted of introducing prey into a naive subject's own home

cage and manually recording the following behaviours: latency to

capture, and the frequency of prey exploration, withdrawal from the

prey, nip at the prey and unsuccessful capture.

The principal findings showed that: 1) older hamsters were

more likely to capture; 2) with the experience of several successful

captures hamsters became more efficient captors; 3) hamsters as

young as 20 days would capture in the normal adult manner; 4) the

interval between successive prey presentations had a small but sig-

nificant effect on the likelihood of capture; 5) prey removal after

capture decreased the chance of subsequent capture in hamsters with

weak dispositions to capture; 6) prey removal after capture had no

effect on hamsters with strong dispositions; 7) the response of

capture could be 'primed' through prior sensory exposure to the prey;
8) prey-capture was susceptible to the effects of selective breeding.

The theory ascribed to these results was that prey-capture in
the hamster was a species-typical behaviour founded upon certain pre-
dispositions but nevertheless liable to the effects of experience.
Therefore it was concluded: 1) for hamsters with weak dispositions
to capture the pre-capture and post-capture experiences were both
needed for the development of the response. The pre-capture phase
(sensory exposure to prey and the performance of the behaviours
involved in capture per se) served primarily to reduce fear and
increase capture efficiency and the post-capture phase (prey consump-
tion) served primarily to increase capture tendency; 2) for hamsters
with strong dispositions to capture the development of predation was
not dependent on eat after capture (the post-capture experience).
This suggested that the pre-capture experience had self-reinforcing
properties of its own.

Hamster predation was then discussed from a comparative viewpoint
and mention was made of areas in need of investigation.