

GROUP SIZE AND FORAGING IN STONELOACH.

Noemacheilus barbatulus.

**A thesis submitted for the degree of
Doctor of Philosophy**

**Nigel E. Street
Department of Zoology
University of Leicester
1985**

UMI Number: U360491

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI U360491

Published by ProQuest LLC 2015. Copyright in the Dissertation held by the Author.
Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code.



ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346



To the memory of my mother

"We shall certainly be roasted or boiled", cried Candide, on noticing the cauldron and the skewers. "What would Professor Pangloss say if he saw how unsophisticated nature behaves? No doubt it is all for the best, but I must say it is very cruel to have lost Lady Cunégonde and to be skewered by the Oreillons".

Voltaire

Acknowledgements

I am very grateful to my supervisor, Paul Hart, for all the help and encouragement that he has given me during the course of this work.

I would also like to thank the following people who have helped me in various ways; Lesley Barnett, John Beckett, Frank Clark, Ian Clarke, Peter Freeman, Steve Ison, Jean Liggins, Anne Magurran, Chris Mills, Ian Parker, Tony Pitcher, Peter Shelton and Hilary Wooden.

This work was supported by an SERC research studentship.

STATEMENT

The accompanying thesis submitted for the degree of Doctor of Philosophy entitled "Group Size and Foraging in Stoneloach, *Noemacheilus barbatulus*" is based on work conducted by the author in the Department of Zoology, of the University of Leicester, during the period between October 1982 and June 1985.

The work recorded in this thesis is original unless otherwise acknowledged in the text or by reference. None of the work has been submitted for another degree in this or any other university.

Signed..........

Date.....23rd August 1985.....

CONTENTS

<u>1</u>	INTRODUCTION: ECOLOGY AND BEHAVIOUR OF STONELOACH	1
1.1	DIET OF STONELOACH	1
1.2	HABITAT OF STONELOACH	2
1.3	BEHAVIOUR OF STONELOACH	4
1.4	DAILY ACTIVITY PATTERNS OF STONELOACH	6
1.5	SOCIAL HABITS OF STONELOACH	8
1.6	STUDY CONTEXT	8
<u>2</u>	GENERAL METHODS	10
2.1	EXPERIMENTAL ANIMALS	10
2.2	TAGGING PROCEDURE	10
2.3	EXPERIMENTAL AQUARIA	11
2.4	VIDEO EQUIPMENT AND LIGHTING SCHEDULE	11
2.5	FOOD PATCHES	12
<u>3</u>	EXPERIMENT 1: GROUP SIZE AND PATCH LOCATION	15
3.1	INTRODUCTION	15
3.2	METHODS	18
3.2.1	Experiment 1A. The effects of group size	18
3.2.2	Experiment 1B. The effects of the amount of food	20
3.2.3	Slow food finders	23
3.3	RESULTS	24
3.3.1	Effects of group size	24
3.3.2	Effects of the amount of food	24
3.3.3	Individual differences in foraging behaviour	28
3.4	DISCUSSION	29
3.4.1	Effects of group size	29

3.4.2	Effects of the amount of food	36
3.4.3	Individual differences in food finding ability	37
<u>4</u>	EXPERIMENT 2: GROUP SIZE AND PATCH EXPLOITATION	39
4.1	INTRODUCTION	39
4.2	METHODS	40
4.3	RESULTS	44
4.3.1	Equal profitability patches	44
4.3.2	Different profitability patches	49
4.3.2.1	Patch visits	49
4.3.2.2	Number of digs	53
4.3.2.3	Group size and time allocation	53
4.3.3	Individual differences in patch exploitation	54
4.3.4	Digging rate	57
4.4	DISCUSSION	64
<u>5</u>	EXPERIMENT 3: GROUP SIZE AND THE IDEAL FREE DISTRIBUTION	70
5.1	INTRODUCTION	70
5.1.1	The ideal free distribution	70
5.1.2	Ideal free searching as an ESS	71
5.1.3	Aggregation and interference	73
5.1.4	Evidence for the ideal free distribution	75
5.2	METHODS	79
5.3	RESULTS	82
5.3.1	Group size, patch profitability ratio and stoneloach distribution	82
5.3.1.1	Ratio of fish between patches	83

5.3.1.2	Distribution of fish over the foraging area	93
5.3.2	Movements between feeding and non-feeding areas	96
5.4	DISCUSSION	103
5.4.1	Stoneloach density and interference between individuals	103
5.4.2	Movements between areas: patch sampling	107
5.4.3	Do the results conform to an ideal free distribution, and if not, why not?	110
<u>6</u>	EXPERIMENT 4: GROUP SIZE AND THE MARGINAL VALUE THEOREM	113
6.1	INTRODUCTION	113
6.1.1	Aims of Experiment 4	113
6.1.2	Optimal allocation of time to patches	113
6.2	METHODS	117
6.3	RESULTS	119
6.3.1	The relationship between residence time and food intake	119
6.3.2	Applying the Marginal Value Theorem	120
6.3.3	Giving Up Time	124
6.4	DISCUSSION	128
<u>7</u>	GENERAL DISCUSSION	131
7.1	The pros and cons of group membership	131
7.2	Group size and patch use	134
7.3	Information and patch use	135
7.4	Stoneloach distribution: an "Ideal Free" distribution?	139

7.5	Suggestions for further study	141
-----	-------------------------------	-----

7.6	Summary of the effects of group size on stoneloach foraging behaviour	143
-----	--	-----

<u>LITERATURE CITED</u>	145
-------------------------	-----

CHAPTER 1

INTRODUCTION: ECOLOGY AND BEHAVIOUR OF STONELOACH

The stoneloach, *Noemacheilus barbatulus* L., is a small bottom-dwelling freshwater fish, belonging to the family Cobitidae. Its' distribution extends from the British Isles eastwards across Europe and Asia (Wheeler 1978). Stoneloach normally attain a maximum length of only 10 to 12cm, although exceptional specimens may measure 15cm (Wheeler 1978).

Studies of the stoneloach have concentrated largely on its ecology, and in particular on its diet and habitat.

1.1 DIET OF STONELOACH

The stoneloaches' diet tends to consist mainly of insect larvae (eg Hartley 1948, Smyly 1955). Sauvonsaari (1971), in his study of stoneloach in southern Finland found that the most important food item was larval Trichoptera; Ephemeroptera nymphs and Chironomid larvae were also important. He suggested that "the food samples seem to show that stoneloach do not select their food, but make use of those food objects which are available and which they chance to observe". In a more recent study of stoneloach in a chalk stream in southern England, Welton, Mills & Rendle (1983) found that larval Chironomidae, Cladocera, Copepoda and some Oligochaeta (in particular various

Tubificidae) accounted for the greatest part of the diet (Table 1.1).

In his study of the feeding relationships between stoneloach, salmon *Salmo salar*, trout *Salmo trutta*, minnows *Phoxinus phoxinus* and three spined stickleback *Gasterosteus aculeatus* in the River Endrick, Scotland, Maitland (1965) suggested that stoneloach selected food passively, the food eaten being dependent largely on the fishes' bottom dwelling habits.

In contrast, Perrin (1980) has shown that stoneloach have distinct dietary preferences, and that they are able to obtain preferred items, such as Chironomid larvae, by choice. Perrin (1980) has also shown that stoneloach are opportunistic feeders, the exact composition of the diet depending to an extent on the invertebrate fauna present. Neveu (1981) also found that stoneloach select preferred items, which were again Chironomids. Hyslop (1981) found that the diet was, in most months, dominated by dipteran larvae, particularly Chironomidae, and that small crustaceans and Oligochaetes were commonly taken.

1.2 HABITAT OF STONELOACH

The stoneloach has been documented in a wide range of habitats. Welton, Mills & Rendle (1983) found that stoneloach showed a preference for areas of soft substratum, particularly when macrophyte vegetation was present. In laboratory experiments, these preferences were

	Jan	Apr	Jun	Aug	Oct	Dec
Nematoda			0.7	2.0		1.2
Gastropoda			2.1	1.3		
Oligochaeta	54.2	54.3	30.7	66.9	19.4	70.6
Plecoptera			1.0			
Coleoptera			2.1			
Trichoptera	1.2	4.8	0.4	0.3	1.4	
Chironomidae	7.8	10.0	8.6	3.0	13.9	3.5
Ceratopogonidae	0.6	5.2	0.7			3.4
Cladocera	12.7	17.1	15.5	0.7	7.0	1.2
Ostracoda				0.3		
Copepoda	20.5	4.3	26.2	13.9	15.3	4.7
<i>A. aquaticus</i>	2.4	2.9	10.7	10.9	29.2	14.1
<i>G. pulex</i>			0.3			2.4

Table 1.1 The number of a particular prey item eaten as a percentage of the total number of prey items. Prey items occurring on only one occasion are not included in the table, but their numbers were included in the total number of prey items eaten. Source: modified from Welton, Mills & Rendle (1983).

again shown. This contrasts with the observations of Sauvonsaari (1971) who found stoneloach on stony shores, or between stones on sandy substrates, but never on a soft substrate. Sterba (1958) reported that the stoneloach also lives on soft substrates, where it may dig into the mud so that only the head protrudes. Smyly (1955) believed the type of substrate to be unimportant, as he found stoneloach on sandy, gravelly and muddy substrates. My own observations, when electrofishing for stoneloach, were that more stoneloach were found in areas of soft substrate, particularly when macrophytes were present, than on sandy or stony substrates.

1.3 BEHAVIOUR OF STONELOACH

The first observations on stoneloach behaviour were made by Bateson (1890), who included the stoneloach in the category of fishes which perceive their food by scent. He observed that "none of these fishes ever start in quest of food when it is first put into the tank, but wait for an interval, doubtless until the scent has been diffused through the water. Having perceived the scent of food, they swim vaguely about and appear to seek it by examining the whole area pervaded by the scent, having seemingly no sense of the direction whence it proceeds". Furthermore, "loaches on perceiving the smell of food hunt for it with their noses and barbels on the bottom".

Smyly (1955) observed that on fine days stoneloach lay in an "apparently dormant state" under stones. At night, or

on dark days, he found them resting on the bottom and occasionally swimming actively to the surface. Smyly agrees with Bateson (1890) that stoneloach do not feed by sight, owing to the dorsal position of the eyes, and to their behaviour whilst feeding.

Filek (1960) also thought that stoneloach found food olfactorily. He noted, however, that they were able to "respond visually at prey and aim at it optically, with particular greed when additionally alerted by olfactory stimuli". Filek (1960) made some detailed, though only qualitative, observations of stoneloach feeding behaviour. Once located, food was obtained by "burrowing" or by "rooting". In the first case, a fish searching for food burrowed into the substrate at the point where the smell of food appeared to be strongest. To do this it positioned its body vertically and pushed down into the substrate with exaggerated wriggling movements. At the start of burrowing the head was pushed sideways, and the tail used to compensate. As the substrate was pushed apart the strokes became more powerful, pushing the fish into the substrate, often as far as the pelvic fins. This sequence took only a few seconds, the fish then sank back to the bottom where it lay still, regardless of whether or not food was found. Then, after a few seconds any food obtained was eaten.

Filek (1960) observed that several individuals frequently burrowed together without disturbing each other. One fish was often seen to copy another, so that it was digging

right alongside the first. Stoneloach were sometimes seen waiting behind the gill slits of individuals which were feeding, apparently for fragments of food which may have passed out.

The second means by which food may be obtained, rooting, is a less energetic activity than burrowing. When rooting a fish swam over a restricted area, picking up mouthfuls of substrate, sorting through it and spitting out anything not required.

Filek (1960) experimentally examined the interaction of olfactory and visual stimuli. He found that stoneloach could "see" food hidden in the gravel, using olfactory stimuli, "as clearly as if it were lying openly on the surface". As previously noted, he found that stoneloach were able to respond to purely visual stimuli, as they snapped at small pieces of sterile wool, which gave no olfactory stimulus. Filek (1960) concluded that a chemical alarm alerts the stoneloach to hunt for food, which is then located using predominantly olfactory cues, visual cues being used to advantage if and when available.

1.4 DAILY ACTIVITY PATTERNS OF STONELOACH

Several studies of the stoneloaches' daily activity pattern have been conducted. The most recent was made by Welton, Mills & Rendle (1983). By positioning the electrodes of a resistivity counter across a large tank of flowing water, records of stoneloach activity were made over a seven day

period, under near-natural conditions. The results clearly demonstrated a large peak of activity at dusk, and for three or four hours following, which gradually declined over the hours of darkness. When the tank was covered with black polythene to exclude the light, there was an immediate increase in activity, which decreased and became sporadic during four days of continuous darkness.

Smyly (1955) recorded that stoneloach remain dormant during the day, only setting out to forage at dusk. However, Sauvonsaari (1971) captured specimens between 1400 and 1600 hrs whose stomachs contained virtually undigested food. He concluded that, as food eaten at night should by this time be fairly well digested, the fish must have been feeding during daylight hours. However Sauvonsaari postulated, by way of explanation, that the findings may have been a result of a seasonal change in the rhythm of food intake, correlated with a successive shortening of day length in September, when the observations were made.

Filek (1960) also found the stoneloach to be active primarily at dusk and dawn. Other studies of the activity patterns of stoneloach have been made by Neveu (1981) and Burdeyron & Buisson (1982). Neveu (1981) described the stoneloach as being strictly nocturnal. Burdeyron & Buisson (1982) also described the activity pattern as being nocturnal, but with an intense period of activity at twilight. When a group of stoneloach were kept in conditions of dim light for a 16 day period, a progressive decrease in the level of locomotor activity was found,

although there was no alteration in the temporal characteristic of the activity. Burdeyron & Buisson therefore postulated that the rhythm was, to some extent, internally controlled. They noted however, that isolated animals did not show such a strictly regular pattern of locomotor activity, the activity of some individuals becoming weaker or arrhythmic after five days under constant conditions.

1.5 SOCIAL HABITS OF STONELOACH

The stoneloach is not a solitary species. Hutchinson (1939) reported large aggregations of over 200 individuals of the loach *Noemacheilus stoliczae* in northern Tibet. While stoneloach have not been found in aggregations of these proportions, several individuals are usually found together, under the same stone, or among a patch of weed (personal observation). Smyly (1955) noted that two or more individuals were often found together under a stone, which was frequently shared with minnows and young trout. According to Smyly, exceptionally large gatherings of stoneloach recorded in Britain have been in response to pollution, and do not normally occur in the clear waters in which stoneloach are usually found.

1.6 STUDY CONTEXT

In this study, some aspects of the foraging behaviour of the stoneloach are examined against a background of optimal foraging theory (eg Pyke, Pulliam & Charnov 1977, Krebs

1978, Krebs & McCleery 1984), which postulates that animals forage so as to maximise their fitness. Additionally an examination of the effects of group size on the foraging behaviour of stone loach is made (see Pitcher (in press) for a summary). Finally, interactions between the effects of group size on foraging, and the predictions made by optimal foraging theory are examined.

CHAPTER 2

GENERAL METHODS

2.1 EXPERIMENTAL ANIMALS

Stoneloach for experiments were obtained by electrofishing from a side stream of the River Welland at Welham, Northamptonshire. Some additional specimens, about 10% of all individuals used, were obtained from the Freshwater Biological Association's River Laboratory at Wareham, Dorset.

In both cases the fish were acclimated to laboratory conditions and a reversed-daylight light regime for at least 30 days before they were used in any experiments. All stock fish were kept in aquaria in the experimental room, which was maintained at 16°C. Thus stock fish were kept under the same conditions as fish in the experimental tanks. The stock fish were fed regularly with tubificid worms. The aquaria were equipped with undergravel filtration, and 40% of the water was changed monthly. All fish used in the trials measured between 8 and 10cm.

2.2 TAGGING PROCEDURE

In some experiments, the subject fish in each group was marked for identification purposes. A small piece of white plastic insulation stripped from electrical wire was used,

measuring 1.5mm in length and 2mm in diameter. This was attached to the fish using very thin nylon, threaded through the caudal peduncle just forward of the tail. The marker was attached whilst the fish was anaesthetised using MS222, and held in a wet net.

2.3 EXPERIMENTAL AQUARIA

All experiments were conducted in aquaria measuring 100 x 30 x 38cm deep. These were fitted with undergravel filters, covered with an 8cm layer of medium grade aquarium gravel. Aged tapwater was used in the aquaria. Monthly water changes of 40% of the tank's volume were made, at the same time the gravel was cleaned using an aquarium vacuum cleaner.

2.4 VIDEO EQUIPMENT AND LIGHTING SCHEDULE

Illumination was given by means of a 300 Watt infra-red (IR) floodlight. The fish were observed using a video camera fitted with a silicon diode tube sensitive to IR light. Either a Canon 16-100mm, F1.9 zoom, or a Cosmincar 8.5mm, F1.5 wide angle lens was used. The camera was fitted with an electronic viewfinder to enable the movement of the fish to be followed during the course of a trial. All trials were recorded on videotape for subsequent analysis.

A reversed-daylight lighting schedule was established, so that "day" was from 2230 until 1030hrs. During the "day"

illumination was provided by two 60 Watt light bulbs positioned 40cm above each aquarium. No illumination was given during the "night" period, when observations were made, except for the IR light used for video recording, and a very dim red light used between trials to give a little light in the experimental room. This latter light was needed as the room would otherwise be too dark to allow the trials to be set up, and was switched off immediately a trial started. A 30min period of "dawn" and "dusk" was simulated by using an automatic electronic dimmer, controlled by a time switch.

The first of a day's trials was started 15min after the lights had fully dimmed (ie 1115hrs), in order to coincide with the fishes' natural period of greatest activity (Welton, Mills & Rendle 1983). The order of trials was randomised to eliminate any possible effects of the time elapsed since the dimming of the lights.

2.5 FOOD PATCHES

Tubificid worms were chosen as the food source in these experiments. Although not generally considered to be the stone loach's most preferred food (eg Smyly 1955, Perrin 1980, Neveu 1981) they are a common component of the fishes' natural diet (see Table 1.1, and Welton, Mills & Rendle 1983), and are, in nature, patchily distributed (Clark & Ison in preparation). Additionally, they were easy to confine to the patches, and burrowed into the gravel in such a way that the fish had to dig into the

substrate to obtain them (Figure 4).

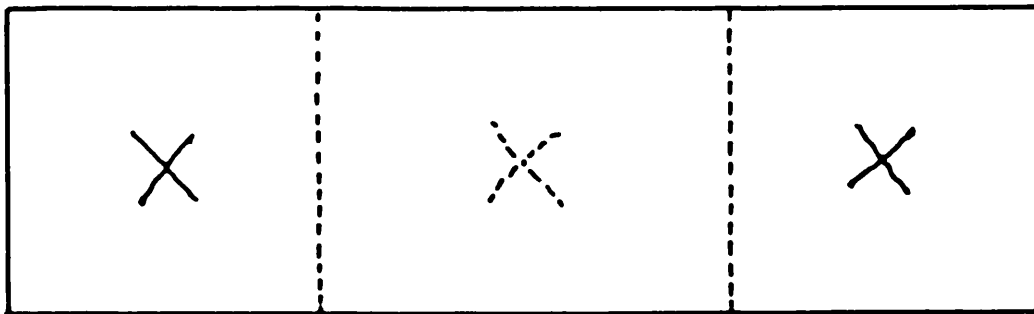
Food patches consisted of plastic petri dish lids, 90mm in diameter and 7mm in depth. These were filled with aquarium gravel of the same type as used in the experimental tanks, and then filled with water. A known amount of mixed tubificid worms was added to the patches approximately 30min before the start of a day's trials. By the end of this 30min period the worms were well dispersed throughout the patch, so that the patches were effectively homogeneous.

The tubificid worms were obtained from "The Underworld", Loughborough. The following four species of tubificid were identified; *Tubifex tubifex*, *Limnodrilus claperedeanus*, *L. hoffmeisteri* and *Potamothrix hammoniensis*.

The worms were accurately weighed on an electronic balance. It was not possible to blot the worms on filter paper before weighing, as this caused them to stick to the paper, and made removal impossible. In lieu of this, a standardised draining procedure was used, where a clump of worms was drained for five minutes between a petri dish bottom and an inverted lid. In this way most of the water was removed from the worms without damaging them.

At the start of each trial, the required number of patches were carefully positioned in the tanks (see Figure 1), and pushed down into the gravel so as to lie flush with the surface.

Figure 1 Plan of experimental aquarium, showing the arrangement of food patches. Broken X= approximate position of the patch in Experiments 1 and 4. Solid X's= approximate position of food patches in Experiments 2 and 3. The broken lines represent the division of the tank in Experiment 3 into two feeding areas, each containing a patch, and a central non-feeding area.



CHAPTER 3

EXPERIMENT 1. GROUP SIZE AND PATCH LOCATION

3.1 INTRODUCTION

A great many species of fish live in social groups, in either co-ordinated and polarised "schools", or in more loosely organised "shoals" (Pitcher 1983). In order for fish to group together, there must be some advantage to be gained, by members of the group. No valid evidence has so far been found to support the hypothesis (eg Weihs 1973) that schooling gives members of the group a hydrodynamic advantage (Pitcher in press). However, several social functions have recently been demonstrated in various species of fish.

It is a commonly held belief that an individual is less likely to be found by a predator if it is a member of a group, because groups will be less easy to find than dispersed individuals, as the groups will be fewer and further between. In many cases this belief is misplaced, as an individual will only be more protected if the predator's feeding rate is lower when feeding on grouped prey (Pitcher in press). In the unlikely case that a predator is able to take only one member of any group discovered, it's success rate will be lower (Bertram 1978), and it will be advantageous to the prey animals to be in a group.

Once a group has been located, the attack success of some predators decreases as the group size of the prey species rises (Neil & Cullen 1974).

An increase in group size also serves to confuse predators (Milinski 1979) as it becomes more difficult to pick a "target" from a mass of similar individuals.

Prey species must be constantly on the lookout for predators. The effects of group size on vigilance have been examined by several authors. When a fish is a member of a group, it needs to spend a smaller proportion of its time being vigilant (Seghers 1981). As a consequence of this, more time is available for foraging (Bertram 1978). Magurran, Oulton & Pitcher (1985) have demonstrated that minnows, *Phoxinus phoxinus*, detected an approaching pike, *Esox lucius*, more rapidly, and ceased to forage later, as shoal size increased.

As well as its influence on an animals' ability to detect and avoid predators, group size has effects on foraging behaviour *per se*. Street, Magurran & Pitcher (1984) have shown that goldfish, *Carassius auratus*, handled their food more rapidly as a result of increasing group size. This was presumably due to greater intra-shoal competition for available food perceived by the fish at larger group sizes. Goldfish in a group of five spent a greater proportion of time foraging, carried out more sampling of patches, and were better at adjusting their foraging activities in

response to changing patch profitabilities than when in a group of two (Pitcher & Magurran 1983). Both goldfish and minnows have been shown to be less timid when in a larger group (Magurran & Pitcher 1983).

Individual goldfish and minnows were able to locate a concealed food source more rapidly when they were a member of a group (Pitcher, Magurran & Winfield 1982). The authors suggested that a member of a foraging group was able to recognise a successful individual, by the way in which it concentrated its' attention on the source of food in the case of minnows, or by the visually-obvious "chomping and chewing" of food in the case of goldfish. According to Magurran (1984), searching goldfish watch for the typical "nose down" posture of a feeding fish.

It is known that stoneloach forage largely by means of olfactory stimuli (Bateson 1890, Smyly 1955, Filek 1960, Welton, Mills & Rendle 1983, amongst others). The following experiment was designed to determine whether or not individual stoneloach were able to find hidden food more rapidly when the number of fish in the group was increased. As the light levels during the experiments were extremely low, visual cues were unlikely to be important to the fish, in contrast to Pitcher, Magurran & Winfield's (1982) goldfish.

For group size to affect the food-finding performance of foraging stoneloach, a searching individual must be able to recognise a successful group member. Due to the low light

available, visual cues should be unimportant, the fish having therefore to rely on alternative cues for recognition of successful fish. The lateral line system of the stoneloach is very well developed (Lekander 1949), and has been shown by Dijkgraaff (1962) to enable the fish to detect moving animals, such as prey, predators or social partners, at close distances. The violent digging used to extract food is likely to cause turbulence in the surrounding water, which may be detectable by other group members, by means of their lateral lines. Other foragers may also be able to hear the sounds of the displacement of gravel made by a digging stoneloach.

Provided that a searching stoneloach is able to recognise a successful individual (a "food finder" (Pitcher in press)), an increase in group size can enhance that individual's chances of finding food, in the following way. With an increase in the density of foragers, the aggregate search rate rises, so that, with the addition to the group of each extra fish, the likelihood of one of the members finding food goes up. This enables initially unsuccessful individuals to benefit by homing in on the food source uncovered by the food finder.

3.2 METHODS

3.2.1 Experiment 1A. The effects of group size

The basic methods used in this experiment were as outlined in Chapter 2. Group sizes of one, two or five individuals

were used, with one of the group marked as described in section 2.2. It proved impossible to study group sizes of more than five fish as the marked individual became too difficult to follow. Five replicate groups were tested, and 10 replicate trials recorded for each group, at each group size.

The behaviour of the subject fish only was scored, the subject fish in each group remaining the same throughout all group sizes. Before recording each 10 day series of trials at a particular group size, a 7 to 10 day acclimatisation period was given, during which the fish were subject to the exact protocol to be used in the forthcoming trials. This ensured that all fish were accustomed to the experimental system, and that, at larger group sizes, later additions to the group were not disadvantaged. It was not possible to distinguish between the behaviour of new and existing group members after this period.

A single, centrally placed, patch was used (see section 2.5 and Figure 1). The exact position of the patch was varied slightly each day in order to allay possible learning effects. Additionally, the order of recording each group was randomised.

0.2g of tubificid worms per fish was given, so that the total varied according to the number of fish in the group and food availability to each fish remained constant. This ensured that motivation and consequent feeding tendency

(see McFarland & Houston 1981) remained constant over the duration of the experiment.

A trial continued until the subject fish had located the patch, with an upper time limit of 15min. Patches were left in place for about 4h, to ensure that the fish had enough time to consume all the available food, and so maintain their long-term hunger level as constant.

The following features of the subject stoneloaches' foraging were recorded.

MOVE. The time after the start of a trial when the fish starts searching for food.

TRAVEL. The time spent moving about in search of food. Travel time started when the fish first moved and stopped when food was found. Periods between the start and finish of travel time when the fish were not actively searching are excluded under this definition.

LOCATE. The total time from the start of a trial until food is found. This definition therefore includes non-searching intervals which occur once searching has commenced.

3.2.2 Experiment 1B. The effects of the amount of food

In Experiment 1A above (section 3.2.1) the amount of food per fish was held at a constant level. Therefore more food

was present at larger group sizes, which could possibly have been easier to detect if olfactory stimuli were involved in food detection. To control for this an experiment was performed with constant group sizes and varying quantities of food. Once again, five replicate groups of fish were tested, and 10 replicate trials recorded for each condition.

Previously untested stone loach were used for each of the three parts of this experiment. A group size of one was given either 0.2 or 1.0g of tubificids, a group size of two either 0.2 or 0.4g, and a group size of five either 0.2 or 1.0g. In this way the extremes of the range of food quantities encountered in Experiment 1A were included. To maintain long term hunger levels, a second patch was added once the first patch had been located. This patch contained 1.0g minus the amount already given. When the first patch contained 1.0g, the second patch contained no further food, but was given in order to maintain the protocol. As the total food given per day is 1.0g, hunger levels at group sizes one, two and five will be different, as the amount of food per fish varies. However this does not matter, as comparisons are needed only between amounts of food *within* a fixed group size.

The design of this experiment is summarised in Table 3.1. The same foraging parameters were recorded as in Experiment 1A, ie MOVE, TRAVEL and LOCATE.

group size	test food quantity	food on 1st patch	food on 2nd patch
1	0.2	0.2	0.8
	1.0	1.0	---
2	0.2	0.2	0.8
	0.4	0.4	0.6
5	0.2	0.2	0.8
	1.0	1.0	---

Table 3.1 Design of Experiment 1B, to determine the effects of the quantity of food on stoneloach foraging. All figures for food quantities are in grammes.

3.2.3 Slow food finders

On some occasions, in both Experiments 1A and 1B, and particularly at a group size of one, the food available was not located within the 15min trial period. On a very few occasions the fish did not move. When the patches were removed from the tank 4h after the time of introduction, disturbance of the gravel in the patch was noticeable. It is therefore fairly safe to assume that the patch had been located and the food exploited (digging actions to obtain food cause disturbance of the gravel surface). According to this assumption, therefore, the patch had been found within 4h but not within 15min.

It was not possible to observe each group for the length of time necessary for the subject fish to find the patch, if that time was greater than 15min, due to the need to run all of the trials within the stoneloaches' natural activity period (see Welton, Mills & Rendle 1983).

To give a more complete result than would be obtained by analysing only those trials completed within 15min, values for move and locate were assigned to trials not completed. The values used were 900sec for move (ie exactly 15min) and 901sec for locate (15min plus 1sec). These values were of course underestimates of those which would have been observed had the trials been recorded until completion. The chosen values were the smallest possible in trials not completed within 15min, and so ensured that an overestimate of move and locate times could not be made, which would in

turn falsely inflate significance values obtained in analysis. As it is, the assigned values gave an underestimate of significance, whilst minimising variances.

With regard to travel time, only those trials completed within 15min were used for analysis. It would be impossible to determine travel times for trials of greater than 15min duration as the proportion of unobserved time spent travelling (as opposed to resting) would be impossible to determine.

3.3 RESULTS

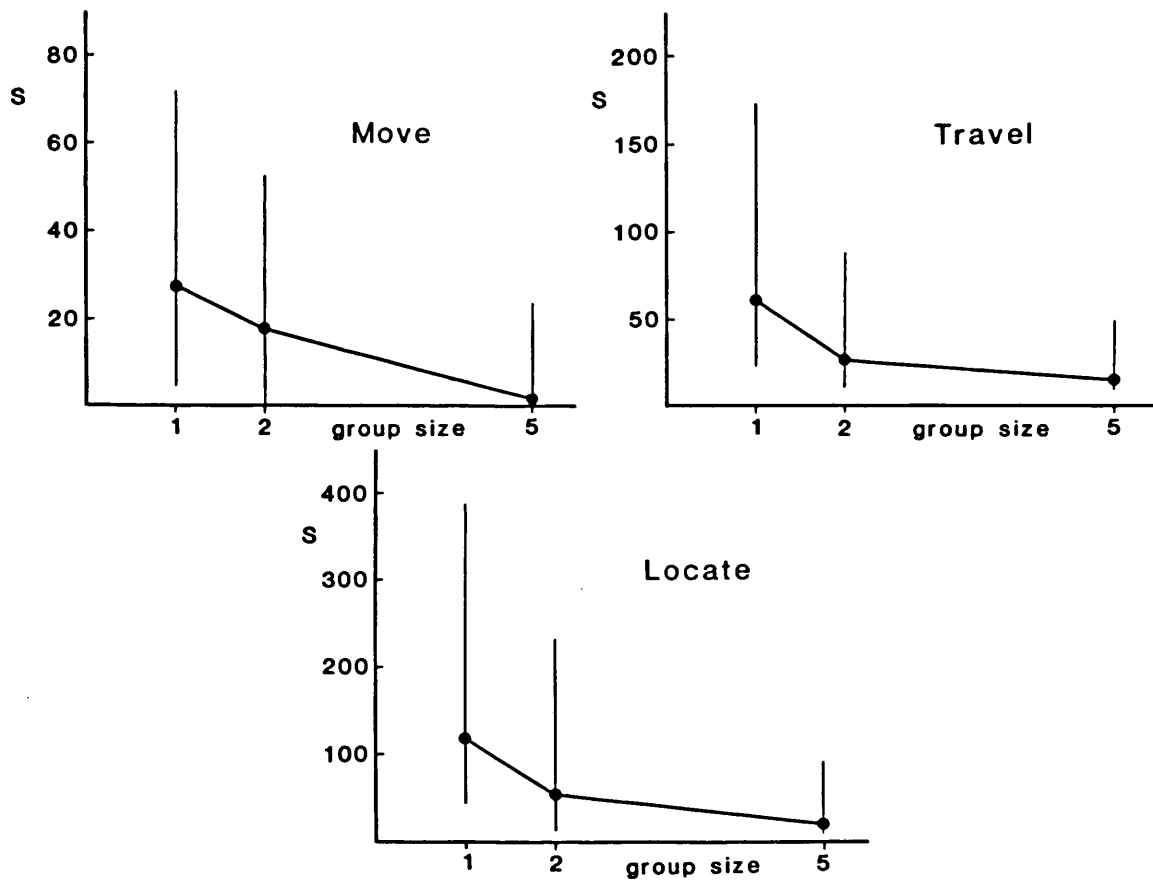
3.3.1 Effects of group size

Results of Experiment 1A, to determine the effects of group size on move, travel and locate times are given in Figure 2. These were analysed using Kruskal-Wallis 1-way ANOVA (Hull & Nie 1981)(Table 3.2). The time taken by the subject fish to locate food decreased dramatically when the group size was increased from one to five individuals. This was due to a reduction in both the time taken before moving out in search of food, and the time spent travelling before food was located.

3.3.2 Effects of the amount of food

The results of Experiment 1B are given in Table 3.3. An increase in the amount of food present caused a reduction in both travel and locate times at a group size of one, but

Figure 2 Effects of group size on the time taken to move, travel time, and the time taken to locate food. Median and quartiles (based on 50 replicates) are shown for each group size.



Kruskal-Wallis ANOVA							
effects of:							
group size				fish		group size	
	1	2	5	χ^2	P	χ^2	P
MOVE	27.50 (900)	17.50 (900)	1.50 (900)	74.23	***	14.23	***
TRAVEL	61.00 (869)	27.00 (399)	14.50 (424)	57.08	***	17.18	***
LOCATE	117.00 (892)	54.00 (899)	21.50 (898)	68.90	***	22.96	***

Table 3.2 Results of Experiment 1A. MOVE, TRAVEL and LOCATE refer to time to move, travel time, and time to locate the patch respectively. Results are given in seconds, as median and range (in parentheses). *** $p < 0.001$.

		Kruskal-Wallis ANOVA						
		effects of:						
		food(g)			fish		food	
group	size	0.2	0.4	1.0	χ^2	P	χ^2	P
1	M	30.50 (900)		27.00 (900)	65.89	***	0.81	NS
	T	69.75 (209)		39.33 (333)	3.23	NS	10.72	***
	L	470.50 (888)		109.25 (896)	60.92	***	5.31	**
2	M	37.50 (900)	43.50 (900)		67.00	***	0.13	NS
	T	32.50 (89)	29.50 (271)		73.74	***	0.06	NS
	L	81.50 (881)	900.60 (894)		3.17	NS	0.87	NS
5	M	8.00 (39)		3.00 (110)	19.36	***	0.55	NS
	T	12.50 (52)		11.00 (23)	4.82	NS	0.67	NS
	L	22.00 (896)		17.75 (898)	19.10	***	1.08	NS

Table 3.3 Results of Experiment 1B. M, T and L refer to time to move, travel time, and time to locate food respectively. Results are given in seconds, as median and range (in parentheses). ** $P < 0.01$, *** $P < 0.001$, NS= not significant.

had no effect on the time taken to move. At group sizes of two and five individuals, the amount of food had no effect on either move, travel or locate times.

3.3.3 Individual differences in foraging behaviour

The main aim of this experiment was to investigate the effects of group size on stoneloaches' ability to locate a hidden food source. Preliminary analysis of the experiment (Table 3.2) revealed highly significant differences between individuals, which could mean either that the fish were not all behaving in the same way, or that they were doing a similar thing but varying widely in the time taken to do it. Table 3.5 shows the latter to be the case; all fish showed a reduction in patch location time with an increase in group size. However, the time to locate the patch varied greatly between individuals. The scale of the decrease was extremely variable, ranging from a 1.9 fold decrease by fish 3, to a 45.5 fold decrease by fish 4 (Table 3.5).

To further investigate the effects of differences in foraging ability, a subsample of 10 trials (trials 1 and 6 for each of the five groups of fish) were analysed in order to determine, for the subject fish, its order of arrival at the patch (abbreviated to OAP). The mean OAP for each fish was calculated, and is given in Table 3.4, together with each fishes' corresponding patch location time at a group size of one. At a group size of two, an OAP of 1 would indicate that the fish was always first, and a value of 2

that it was always last. At a group size of five, where the subject fish may come anywhere between first and fifth, the OAP can range from 1 to 5. The frequency of each OAP is shown in Figure 3, for each fish. These values were used to determine the mean OAP's given in Table 3.4.

The OAP for each fish at each group size was correlated with that individual's patch location time when alone (ie in a group size of one), using Spearman's Correlation Coefficient (Lehner 1979). A significant correlation was found for group sizes of both two and five individuals (group size of two; $r_s = 0.90$, $P < 0.05$, group size of five; $r_s = 0.90$, $P = 0.05$). This indicates that a fish showing a long locate time when alone (ie a poor food finder) retained its' poor performance when in a larger group.

3.4 DISCUSSION

3.4.1 Effects of group size

The results of this experiment indicate that stoneloach were able to locate a concealed food source more rapidly as group size increased from one to five individuals. This overall effect may be broken down into two components.

Firstly, the fish started out in search of food sooner after the start of a trial, once food was introduced. Secondly, travel time was reduced.

A reduction in the time taken to move as group size

Fish	Locate time at G.S. 1	OAP at G.S. 2	OAP at G.S. 5
5	120.2	1.3	1.4
2	137.4	1.3	1.9
3	255.2	1.6	4.1
4	742.2	1.6	2.3
1	754.2	2.0	4.3

Table 3.4 Mean OAP at group sizes of two and five. Locate times are given in seconds. G.S. = group size. See text for explanation.

Group Size	Fish				
	1	2	3	4	5
1	754.20 (298.37)	137.40 (271.55)	255.20 (341.74)	742.20 (335.45)	120.20 (275.01)
2	736.20 (245.54)	10.50 (3.92)	216.20 (251.14)	103.50 (121.27)	22.50 (28.37)
5	325.40 (353.07)	9.30 (2.50)	137.70 (127.03)	16.30 (11.11)	30.70 (30.29)

Table 3.5 Locate time of each individual at each group size, given in seconds as mean and standard deviation (in parentheses).

group size	food (g)	% fish not moving	% fish not locating
------------	----------	----------------------	------------------------

E X P E R I M E N T 1A

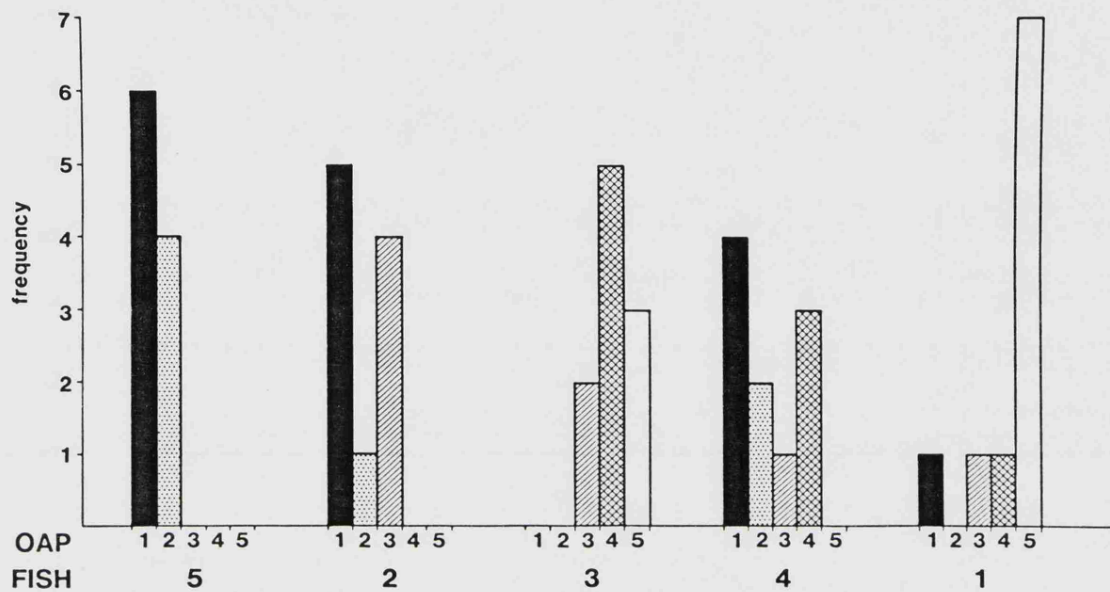
1	0.2	4	36
2	0.4	2	14
5	1.0	0	2

E X P E R I M E N T 1B

1	0.2	0	4
	1.0	0	16
2	0.2	22	32
	0.4	46	56
5	0.2	4	48
	1.0	16	32

Table 3.6 The proportion of trials in which fish did not move, or locate food.

Figure 3 Frequency distribution of the order of arrival at the patch (OAP) at a group size of five (see text for explanation).



increased may be explained in terms of the aggregate food detection capability of the group. When a single fish is present it must rely on itself to detect any food. However, when other individuals are present, another fish may detect the food, and respond to it by starting to forage. Therefore, as long as one stoneloach is able to detect the movements of another, it has potential access to an additional source of information.

As the stoneloach were foraging by non-visual means, the distance of a fish from the food would have affected the individual's ability to detect it. For example, an olfactory stimulus will take time to diffuse through the water, and individuals furthest from the food should therefore take longer to detect it.

Bateson (1890) observed that stoneloach waited for an interval once food had been introduced "doubtless until the scent has been diffused through the water". When only a single fish was present its response could be to the food only, there being no other relevant stimulus. When more than one fish was present an individual could respond to movements of other group members, who had already detected the food, rather than to the food itself. In this way the first fish to detect the food could alert other group members to its presence inadvertantly, merely by starting to forage. This does not imply an active transfer of information, and it would possibly be disadvantageous for the detector to alert others to a finite food resource. The transfer is more likely to be a passive process

(Pitcher, Magurran & Winfield 1982) where individual fish use the behaviour of conspecifics to detect food.

The stoneloach has a well developed lateral line system (Lekander 1949) which can be used to detect moving animals at close distances (Dijkgraaf 1962), so it seems reasonable to assume that the fish were able to detect each others' foraging movements within the limited confines of the experimental tanks. For example, violent digging movements were used to extract worms from the patch. It seems unlikely that the sounds of rummaging in the gravel would have been significant in guiding others to a successful feeder, as the airlifts of the filtration system used produced a lot of noise above which sounds of feeding may have been difficult for the fish to hear. For recent reviews on the roles of olfaction and the lateral line in fish behaviour see Hara (in press) and Bleckmann (in press) respectively.

The reduction in travel time with increasing group size may be explained in a similar way. Although explicit measurements were not made, the fish did not appear to move more rapidly. Therefore, in order to reduce travel time, a more direct route to the patch must have been taken. Information received from the location of other individuals would be a way in which such a change could be caused. Observations made during trials frequently revealed individuals apparently following one another.

3.4.2 Effects of the amount of food

The results given in Table 3.3 show that, at a group size of one, an increase in the amount of food available from 0.2 to 1.0g led to a decrease in both travel and locate times. The time taken before first moving out in search of food remained unaffected by the increase in food quantity. A primarily non-visual feeder such as the stoneloach (Smyly 1955, Filek 1960, Sauvonsaari 1971) might be expected to be capable of differentiating between different quantities of concealed food olfactorily. As already noted, Filek (1960) observed that stoneloach were able to "see" food hidden in the gravel "as clearly as if it were lying openly on the surface", by means of olfactory stimuli.

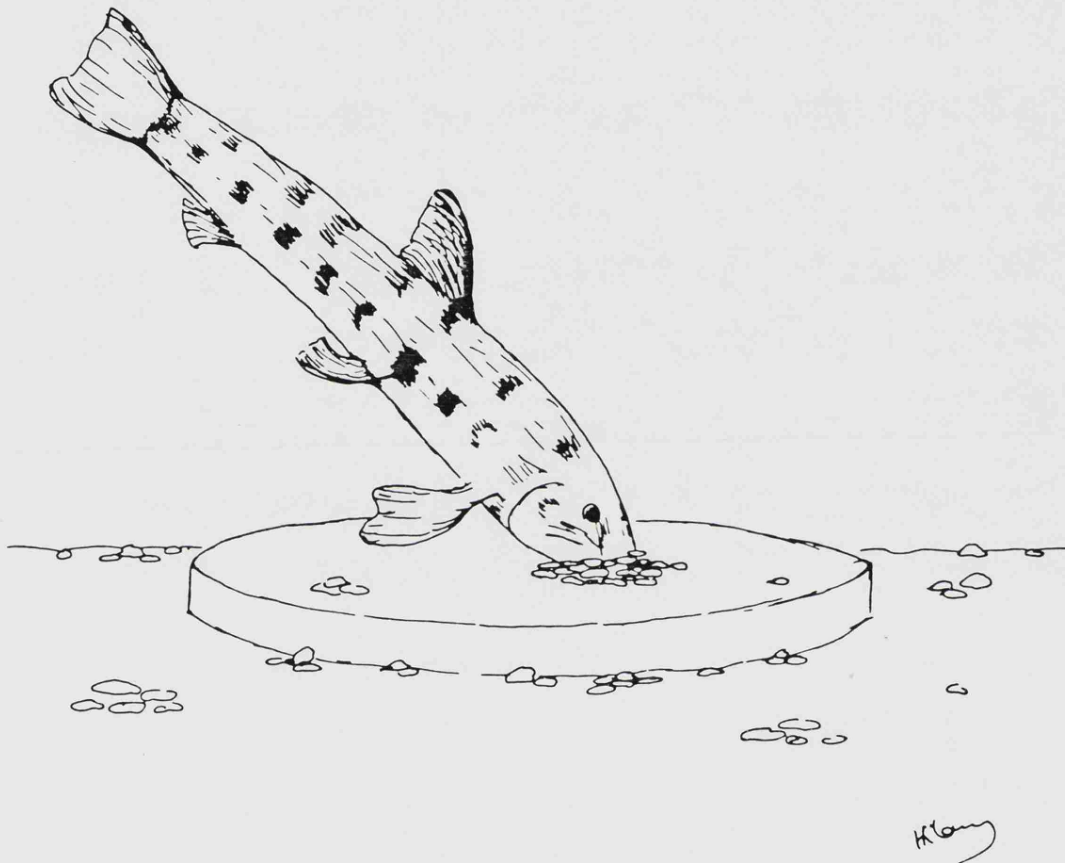
An increase in the amount of food from either 0.2 to 0.4g or from 0.2 to 1.0g had no effect on the food-finding abilities of the subject fish at group sizes of both two and five individuals (Table 3.3). Together with the results obtained at a group size of one, it is apparent that a single stoneloach found a larger amount of food more easily, presumably by means of the greater olfactory stimulus produced, but when conspecifics were present (at group sizes of two and five) the social advantage of improved food location overrode the effect of a greater olfactory stimulus produced by a larger amount of food.

3.4.3 Individual differences in food-finding ability

Each individuals' initial food-finding performance (as indicated by its' patch location time when in a group of one) was retained as group size was increased (Table 3.5). In other words, although all fish benefitted from an increase in group size, poor finders remained poor. This would suggest that a poor finder has more to gain from group membership than a good finder, although the overall level of benefit would decrease with an increasing proportion of poor finders in the group. In this experiment the greatest benefit, in terms of a reduction in the time taken to locate food was achieved by fish 4, an initially poor finder. However, the second greatest benefit was obtained by fish 2, an initially good finder.

It seems likely that in the wild the proportions of stone loach of different food-finding abilities will alter until they reach a stable point at which the gain to all individuals is equal (Barnard & Sibly 1981). In their natural habitat stone loach would be free to associate with conspecifics of their choice, not just those with whom they were placed, as was the case in these experiments. However, the members of each group were drawn from a large stock, so it is hoped that each group contained fish covering at least part of the naturally occurring range of food-finding ability. This would seem to have been so, indicated by the significant correlation between initial food-finding ability and mean OAP at the larger group sizes.

Figure 4 A stoneloach in the typical digging position used to obtain worms from the patch. In experiments the patches were pushed down into the gravel to lie flush with the surface. Drawing by Hilary Wooden.



CHAPTER 4

EXPERIMENT 2. GROUP SIZE AND PATCH EXPLOITATION

4.1 INTRODUCTION

In the previous experiment (Chapter 3) it was shown that stoneloach were able to locate a hidden food source more rapidly when they belonged to a larger group of individuals. In this chapter, the effects of group size on patch exploitation are examined; the two patches being of either equal or different profitability.

A considerable amount of work has been carried out to examine the costs and benefits of group living in various bird species (eg Kenward 1978, Caraco 1979, 1980, 1983, Barnard 1980, Bertram 1980, Studd, Montgomerie & Robertson 1983, Caraco & Chasin 1984), but rather less on the functions of fish shoals.

However, various social advantages for fish living in groups have recently been demonstrated. As previously noted, individual goldfish, minnows (Pitcher, Magurran & Winfield 1982) and stoneloach (Street & Hart in press) were able to locate a hidden food source more rapidly as group size increased. Pitcher & Magurran (1983) have shown that goldfish in a group of five individuals spent a greater proportion of their time foraging, and were more responsive to changes in patch profitability, than when in a group of

only two fish.

Both goldfish and minnows were less timid at larger group sizes (Magurran & Pitcher 1983), and consequently paid longer visits to food patches as group size increased. Foraging minnows detected an approaching model pike sooner, but remained on the patch longer when group size increased (Magurran, Oulton & Pitcher 1985), while sticklebacks, *Gasterosteus aculeatus*, were more ready to approach an area of high predator risk, away from cover, at a larger group size (Milinski in press).

The conflicting demands for foraging and vigilance have been examined by several authors (eg Sih 1980, Lendrem 1983, see Hart in press). From these studies, and those of Kenward (1978), Caraco (1979), Bertram (1980) and Seghers (1981) it appears that as group size increases, each individual's need to be vigilant decreases, and so more time becomes available for foraging. For example, Caraco, Martindale & Pulliam (1980) found that individual Yellow-eyed Juncos, *Junco phaeonotus*, spent more time feeding in a flock than when alone when nearby cover was absent. This was due to a reduced need to scan for predators when feeding in a flock.

4.2 METHODS

The basic methods used in this experiment were as outlined in Chapter 2. The effects of group size on patch exploitation were examined, where two patches, of either

equal or different profitability were present. Group sizes of either two or five individuals were used, and patch profitabilities of either 1:1 or 4:1. A profitability ratio of 4:1 was chosen in the hope of obtaining less equivocal results than might have been obtained had the difference between patch profitabilities been smaller.

Five replicate groups of fish were tested (but see below), and 10 replicates obtained from each group at each group size. The behaviour of the subject fish in each group was scored, the subject fish remaining the same over both group sizes. This individual was marked as described in section 2.2.

During the course of the trials at the larger group size (five fish) with equal profitability patches, fish 5 died. As there was insufficient time available to repeat the experiment with an extra fish, data obtained at a group size of two from fish 5, before it died, were disregarded. The following analyses of the experiment with equal profitability patches are therefore based on four groups of fish.

Before recording a 10 day set of replicates, the fish were acclimatised to the experimental protocol for between 7 and 10 days. This ensured that group members were accustomed to the system and that, at the group size of five (formed by adding three new fish to the existing group of two), the later additions to the group were not at a disadvantage. Differences in behaviour between the new and established

group members could not be distinguished after this period.

Two patches were used, as described in section 2.5. 0.2g of tubificid worms per fish were used, the total amount being divided between the patches in accordance with the profitability ratio under examination (ie 1:1 or 4:1). This amount had been predetermined as that required to maintain an intermediate hunger level, whilst not allowing the fish to reach satiation. The two patches were placed at opposite ends of the tank (Figure 1), and the order of patch introduction alternated in order to prevent the fish from learning which patch was introduced first. Additionally, the order of recording of the five groups was randomised, to control for effects of the length of time after dimming of the lights.

Each trial lasted for 15min, but the patches remained in place for about 4h afterwards, to enable the fish to consume all of the available food. This should have maintained their hunger level and consequent feeding tendency (McFarland & Houston 1981) at a constant level over the duration of the experiment.

Foraging at the patch profitability ratio of 1:1 was examined first, followed by the 4:1 ratio. A new stock of fish were used for the latter part of the experiment, to avoid the reuse of experienced fish.

The following features of the stoneloaches' foraging behaviour were recorded.

At a patch profitability ratio of 1:1...

NUMBER OF DIGS. The number of digs made during a trial.

PATCH VISITS. The number of separate visits made to both patches. Only visits where exploitation occurred are included, ie where digs were made.

PATCHES VISITED. Whether no patches, one patch, or two patches were visited during the course of a trial.

SWITCHES. The number of times a fish ceased to exploit one patch and started to exploit the other. Instances when a fish left a patch and then returned to the same one are not included.

At a patch profitability ratio of 4:1...

NUMBER OF DIGS (LOW). The number of digs made on the low profitability patch.

NUMBER OF DIGS (HIGH). The number of digs made on the high profitability patch.

PATCH VISITS (LOW). The number of separate visits made to the low profitability patch. Only visits where exploitation occurred are included.

PATCH VISITS (HIGH). The number of separate visits made

to the high profitability patch. Only visits where exploitation occurred are included.

4.3 RESULTS

4.3.1 Equal profitability patches

The results of this experiment are given in Table 4.1, together with the results of 2-way ANOVA's, and illustrated graphically in Figure 5. There was an increased total number of separate visits to the two patches as group size increased from two to five individuals. These visits were of a shorter duration (mean for groups of 2 = 53.9s, mean for groups of 5 = 18.75s, $P < 0.001$, t-test). The combined effect, therefore, was that individuals made a greater number of shorter visits to the patches at the larger group size. The relative frequency of visit durations is shown graphically in Figure 6, for group sizes of both two and five individuals.

In order to determine whether the presence of other fish on the patch affected an individual's feeding behaviour, a subsample of 10 trials at each group size (trials 1 and 6 for each of the five groups of fish) was examined. The mean number of digs per visit made by the subject fish with and without conspecifics on the patch was then determined. No significant difference was found at either a group size of two (without conspecifics = 4.47 digs per visit, with conspecifics = 4.13 digs per visit, $0.9 > P > 0.5$, t-test) or a group size of five (without conspecifics = 1.5 digs per

	group size	individual	interaction
digs	NS	***	***
total patch visits	***	***	**
patches visited	***	***	NS
switches	***	***	*

Table 4.1 The effects of group size on the exploitation of two patches of equal profitability. Results are from 2-way ANOVA. N=50 (5 groups x 10 replicates). *P<0.05, **P<0.01, ***P<0.001, NS=not significant.

Figure 5 Effects of group size on the number of digs, the number of visits to the patches, the number of patches visited, and the number of switches between patches, where patches were of equal profitability. Mean and S.E. are shown. See text for an explanation of terms.

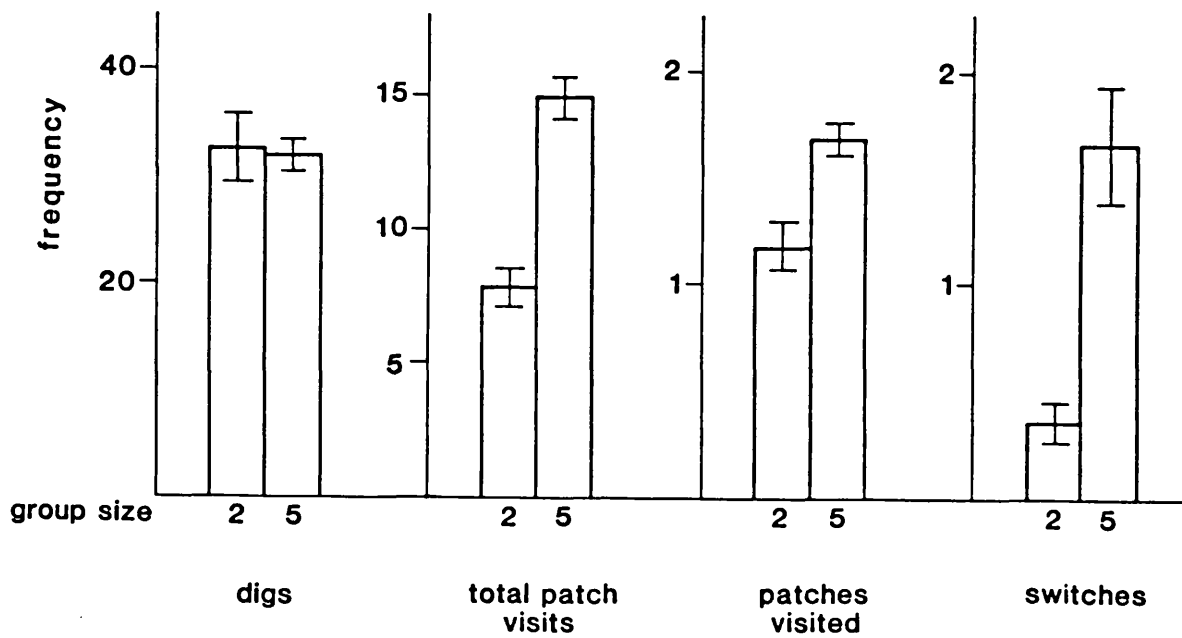
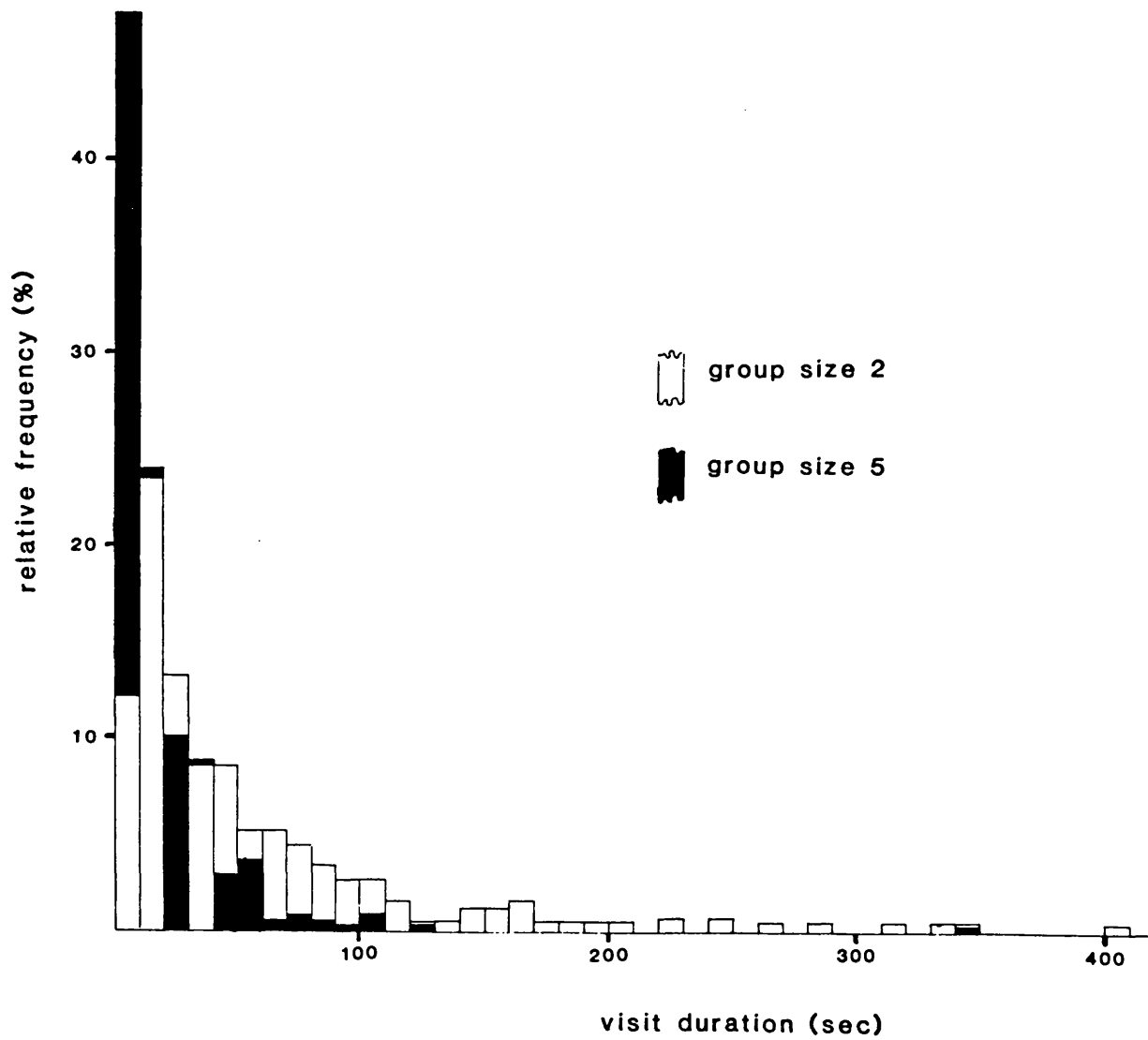


Figure 6 Relative frequency of visit duration (10sec class interval) at group sizes of two and five individuals, where patches were of equal profitability.



visit, with conspecifics = 2.06 digs per visit, $0.5 > P > 0.4$, t-test). These results also demonstrate a reduction in the number of digs per visit at the larger group size.

The increase in group size did not alter the total number of digs made during a trial (Table 4.1). As food could only be obtained by digging into the patches, it is tentatively assumed that the fishes' total food intake was unaffected by an increase in group size. The relationship between the number of digs made and the quantity of food obtained will be examined in detail in Experiment 4 (see Figure 19). However, it is not known if digging efficiency was the same at both group sizes, and this information would be necessary in order to state with certainty whether the fishes' food intake was the same at both group sizes.

The number of patches visited per trial (of the two present), and the number of switches per trial both increased with a rise in group size, suggesting that individuals may have increased their sampling of the patches. The rate of digging whilst on a patch also increased with group size (mean for groups of 2 = 0.104 digs per sec, mean for groups of 5 = 0.182 digs per sec, $P < 0.001$, t-test).

The general conclusion which can be drawn from this section of the experiment is that at the larger group size of five individuals increased their activity in general, and the number of visits made to the patches particular, but did not suffer a consequent reduction in food intake. It is

possible that an increase in sampling (see below) may enable foragers to detect more easily the better patches in an environment of varying patch quality. This hypothesis is examined in the second section of this experiment, where two patches of different profitability were available.

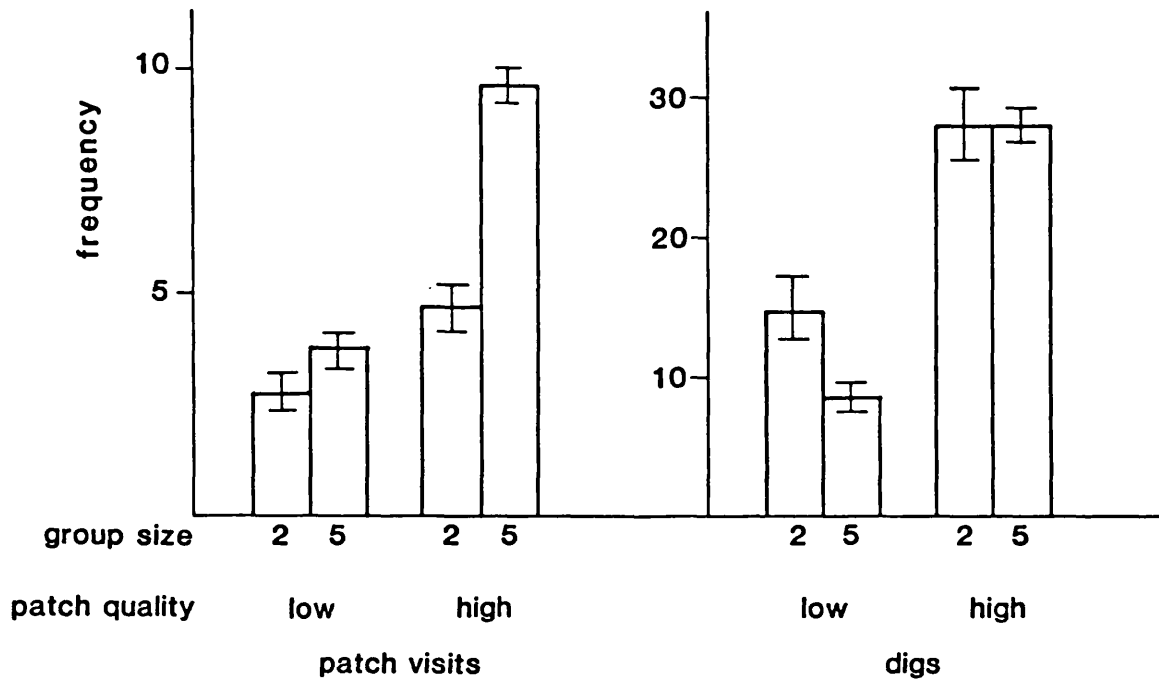
4.3.2 Different profitability patches

4.3.2.1 Patch visits

The number of visits made to the two different profitability patches (Figure 7) was analysed using 2-way ANOVA (Table 4.2). The number of visits made to both high and low profitability patches increased when group size was increased from two to five individuals. From Figure 7 it is apparent that the increase on the good patch was considerably greater than that on the poor patch. When data for both patches was combined, a significant increase in the total number of visits made to the patches with increasing group size was found ($P < 0.001$, Table 4.2). This result is similar to that found in section 4.3.1 above, where both patches were of equal profitability.

As the total number of visits increased with group size, but the total time spent on the patches decreased (see Figure 8), indicating overall a greater number of shorter visits, the fish would have had a greater opportunity to sample the environment at the larger group size. The occurrence and role of sampling in foraging will be discussed further in Chapter 5.

Figure 7 Effects of group size on the number of visits to, and digs made on, the high and low profitability patches. Mean and S.E. are shown.

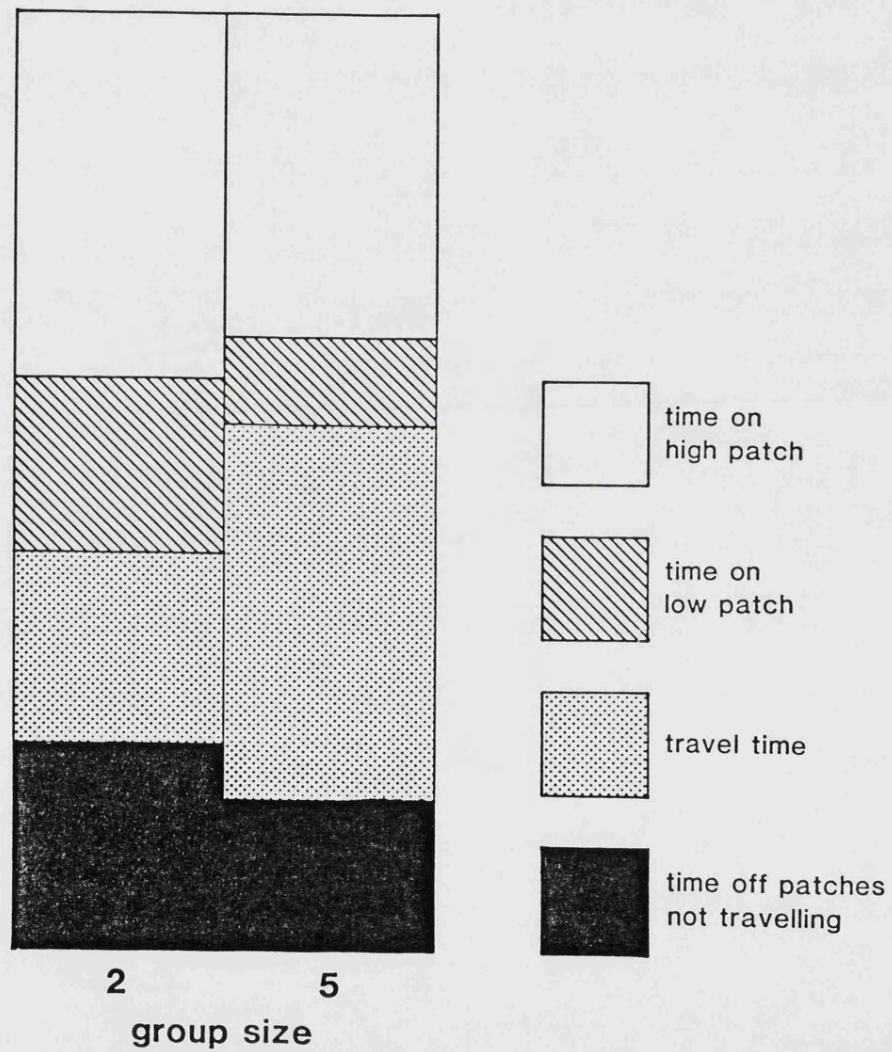


	group size	individual	interaction
patch visits (low)	*	**	NS
patch visits (high)	***	***	**
total	***	***	***
digs (low)	**	*	NS
digs (high)	NS	*	***
total	***	***	***

Table 4.2 The effects of group size on the exploitation of two patches of differing profitability (1X and 4X). Results are from 2-way ANOVA. N=50 (5 groups x 10 replicates). Low and high refer to 1X and 4X patch profitabilities respectively. Data for patch visits (low) were normalised by transformation to square roots.

* P<0.05, ** P<0.01, *** P<0.001, NS=not significant.

Figure 8 Effects of group size on time allocation during a 900sec trial to foraging on the high or low profitability patches, travel, and time spent off the patches and not travelling.



4.3.2.2 Number of digs

When group size was increased from two to five fish, there was no change in the number of digs made on the good patch, but the number made on the poor patch decreased significantly ($P < 0.01$, Table 4.2). When values for the total number of digs made on the two different profitability patches were combined to give an overall value for both patches, a significant ($P < 0.001$) decrease was found, indicating that individuals made a smaller total number of digs at the larger group size.

As fewer digs were made, individuals therefore had fewer food-finding opportunities. If the effects of an increase in group size are to be beneficial, this apparent cost must be outweighed by some benefit. So far no quantitative measure of the amount of food obtained per dig has been made. This problem is examined in Chapter 6. Although the amount of food obtained per dig is as yet unknown, it is intuitively likely that if a fish makes fewer attempts at obtaining food it has a smaller chance of obtaining any.

4.3.2.3 Group size and time allocation

The way in which the fish allocated their time between different activities at group sizes of two and five individuals, where the patches differed in profitability, is shown in Figure 8. A significant increase in travel time occurred when group size was increased from two to

five individuals (mean for groups of 2= 186.0s, mean for groups of 5= 363.4s, $P < 0.001$, t-test). This was accomplished at the expense of a reduction in the time spent on the poor patch (mean for groups of 2= 163.4s, mean for groups of 5= 78.6s, $P < 0.01$, t-test). No significant changes occurred in either the time spent feeding on the good patch (mean for groups of 2= 349.0sec, mean for groups of 5= 311.9sec, $0.4 > P > 0.2$, t-test), or the time spent neither searching nor feeding (mean for groups of 2= 198.7sec, mean for groups of 5= 142.9sec, $0.1 > P > 0.05$, t-test).

4.3.3 Individual differences in patch exploitation

As in the previous experiment (Chapter 3), significant differences were found between the behaviour of individual fish, both when the patches were equal, and when different in profitability. This, however, does not detract from the significance of the results obtained for the effects of group size, as the component of the ANOVA's for group size effects was recalculated against the interaction, if the latter was found to be significant (Sokal & Rohlf 1981). The P-values for the effects of group size given in Tables 4.1 and 4.2 are shown after recalculation in this way.

The behaviour of each individual is given in Tables 4.3 (equal profitability patches) and 4.4 (different profitability patches). In nearly every instance, all individuals showed the same qualitative change in behaviour (ie that behaviour increased, decreased, or remained

Group Size	Fish			
	1	2	3	4
NUMBER OF DIGS				
2	37.50 (14.92)	43.40 (5.44)	43.10 (14.29)	6.00 (7.69)
5	32.10 (5.74)	30.30 (5.44)	41.60 (7.12)	23.30 (8.34)
TOTAL PATCH VISITS				
2	8.30 (2.71)	12.50 (4.14)	8.10 (3.81)	2.40 (2.68)
5	14.00 (3.74)	16.30 (2.45)	20.20 (4.26)	9.00 (2.91)
PATCHES VISITED				
2	1.40 (0.52)	1.30 (0.48)	1.50 (0.53)	0.50 (0.53)
5	1.80 (0.42)	1.80 (0.42)	1.90 (0.32)	1.20 (0.42)
SWITCHES				
2	0.50 (0.71)	0.30 (0.48)	0.60 (0.70)	0.00 ----
5	1.70 (1.16)	1.90 (1.52)	2.80 (2.10)	0.20 (0.42)

Table 4.3 Foraging behaviour of each individual at each group size, when patches were equal in profitability. Results are given as mean and standard deviation (in parentheses).

Group Size	Fish				
	1	2	3	4	5
VISITS TO LOW (1X) PROFITABILITY PATCH					
2	3.60 (2.55)	2.70 (1.70)	0.75 (1.17)	3.20 (3.01)	3.10 (3.31)
5	3.70 (2.83)	4.70 (2.79)	1.30 (2.11)	3.80 (2.04)	5.10 (2.23)
VISITS TO HIGH (4X) PROFITABILITY PATCH					
2	4.40 (2.46)	5.40 (2.12)	2.75 (2.38)	1.90 (2.64)	8.60 (4.88)
5	11.80 (2.66)	10.80 (2.53)	6.00 (2.58)	9.00 (2.63)	10.20 (1.93)
<hr/>					
DIGS ON LOW (1X) PROFITABILITY PATCH					
2	19.70 (13.80)	18.90 (10.02)	5.50 (7.86)	19.30 (18.07)	8.60 (10.32)
5	10.20 (8.68)	10.30 (7.50)	4.60 (7.29)	8.20 (4.49)	9.90 (5.53)
DIGS ON HIGH (4X) PROFITABILITY PATCH					
2	29.70 (15.80)	41.20 (11.61)	21.75 (16.66)	14.90 (21.39)	31.40 (10.94)
5	33.40 (9.01)	26.10 (5.74)	32.80 (5.85)	26.80 (8.77)	20.80 (7.67)

Table 4.4 Foraging behaviour of each individual at each group size, where patches were different in profitability. Results are given as mean and standard deviation (in parentheses).

unchanged). However, there were in general large quantitative differences between individuals, which account for the significant differences between individuals shown in Tables 4.1 and 4.2.

As, in most cases, the behaviour of all individuals was affected by an increase in group size in a similar way (but with quantitative differences), a discussion of the overall effects of group size without a detailed examination of individual differences is possible. However, one individual difference worth noting is that, at the 1:1 profitability, the overall "performance" of fish 4 seems markedly inferior to that of the other three fish.

4.3.4 Digging rate

The effect of elapsed time on the fishes' digging rate (measured as digs per second while on the patch) was examined at each group size. When patches were equal in profitability, no effect was found at a group size of two (Figure 9), but a significant decrease in digging rate occurred at a group size of five (Figure 10).

The relationship between digging rate and visit length, measured in terms of the number of digs made during a visit, was then examined where the patches were different in their profitabilities. Results for each group size and patch profitability (1X or 4X) are given in Figures 11 to 14. In all four cases, digging rate decreased significantly as visit length increased.

Figure 9 The relationship between digging rate and elapsed time during a trial, at a group size of two and where patches were of equal profitability. The digging rate is plotted against the mid-point time of the corresponding patch visit. The regression line and 95% confidence limits are plotted. ($n=272$, $b=-0.00002$, $R=0.08$, $F=1.89$, $P=0.17$).

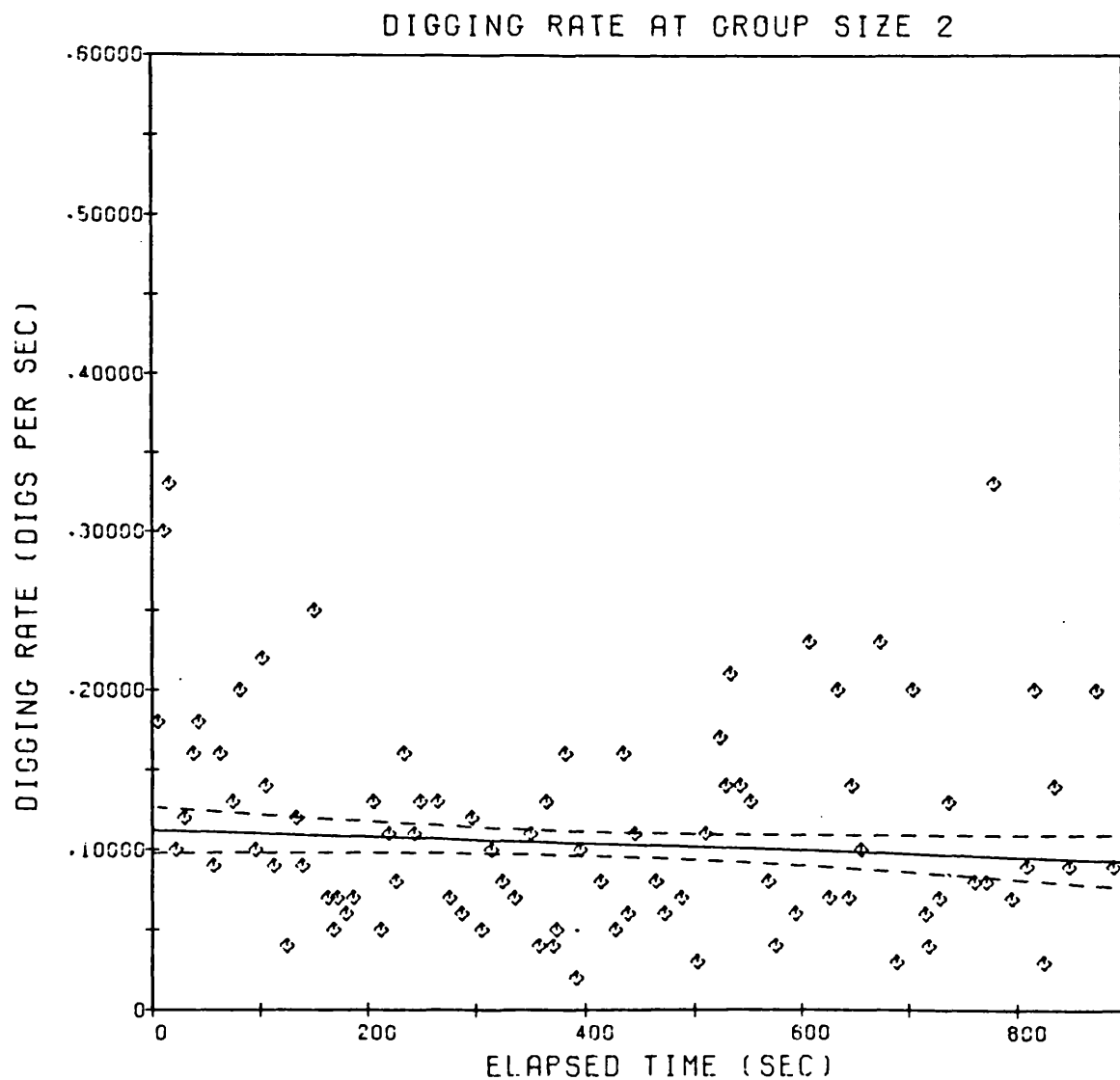


Figure 10 The relationship between digging rate and elapsed time during a trial, at a group size of five and where patches were of equal profitability. The digging rate is plotted against the mid-point time of the corresponding patch visit. The regression line and 95% confidence limits are plotted. ($n=381$, $b=-0.00009$, $R=0.19$, $F=13.51$, $P<0.0001$).

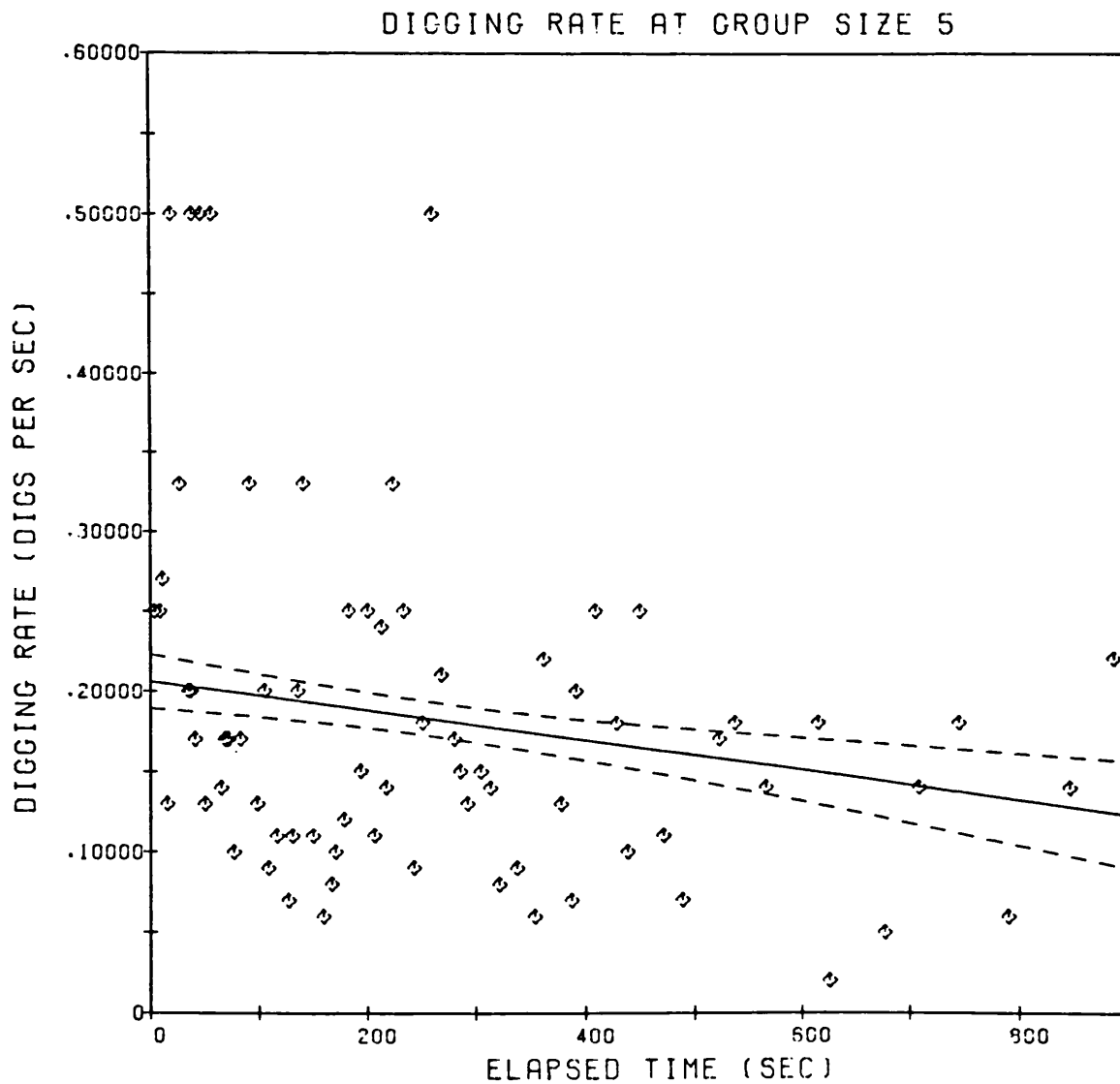


Figure 11 The relationship between digging rate and the number of digs made during a visit, on the low profitability patch at a group size of two. Patches differed in profitability. The regression line and 95% confidence limits are plotted. ($n=127$, $b=-0.003$, $R=0.29$, $F=11.44$, $P<0.0001$).

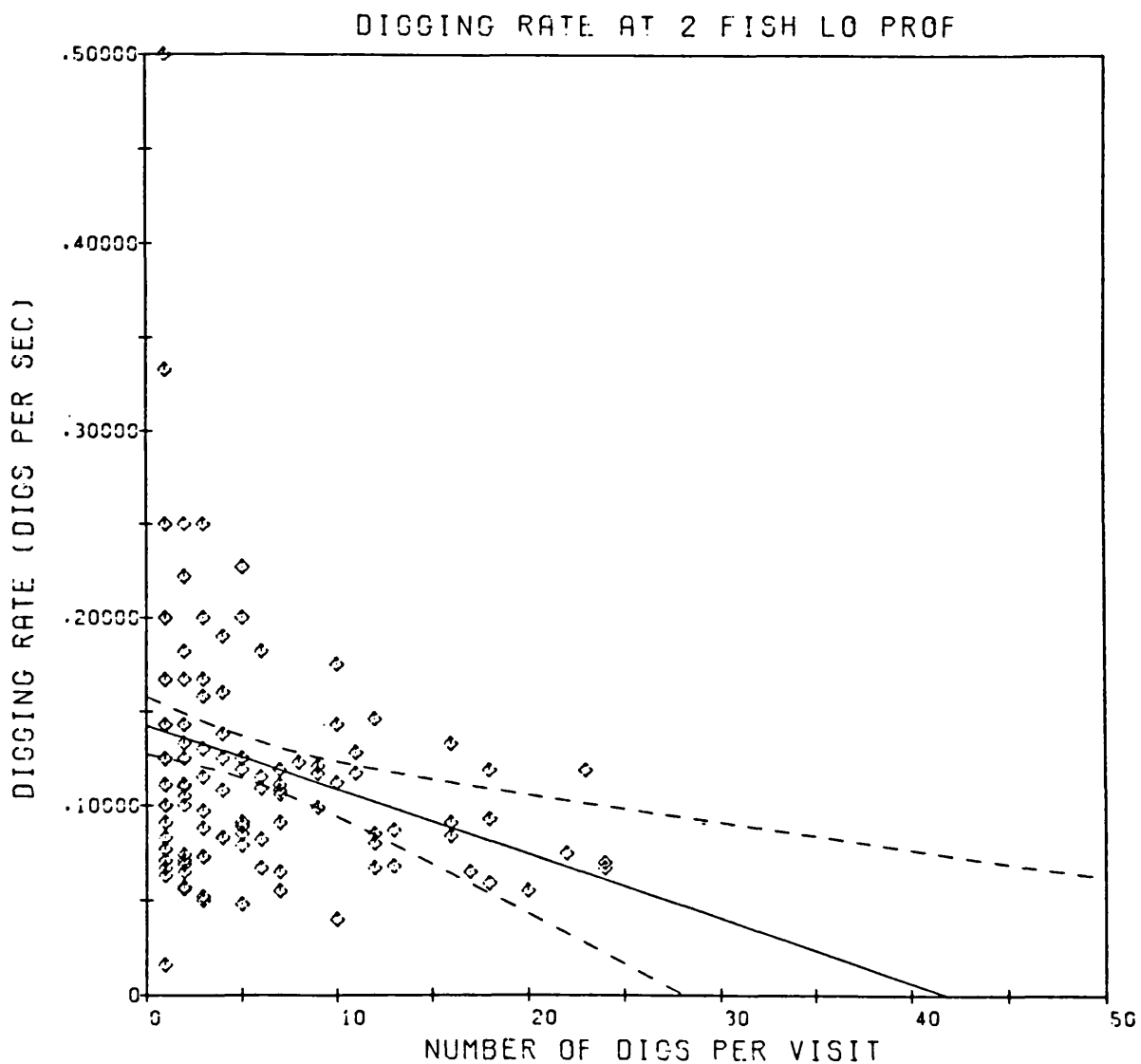


Figure 12 The relationship between digging rate and the number of digs made during a visit, on the high profitability patch at a group size of two. Patches differed in profitability. The regression line and 95% confidence limits are plotted. ($n=206$, $b=-0.003$, $R=0.28$, $F=17.26$, $P<0.0001$).

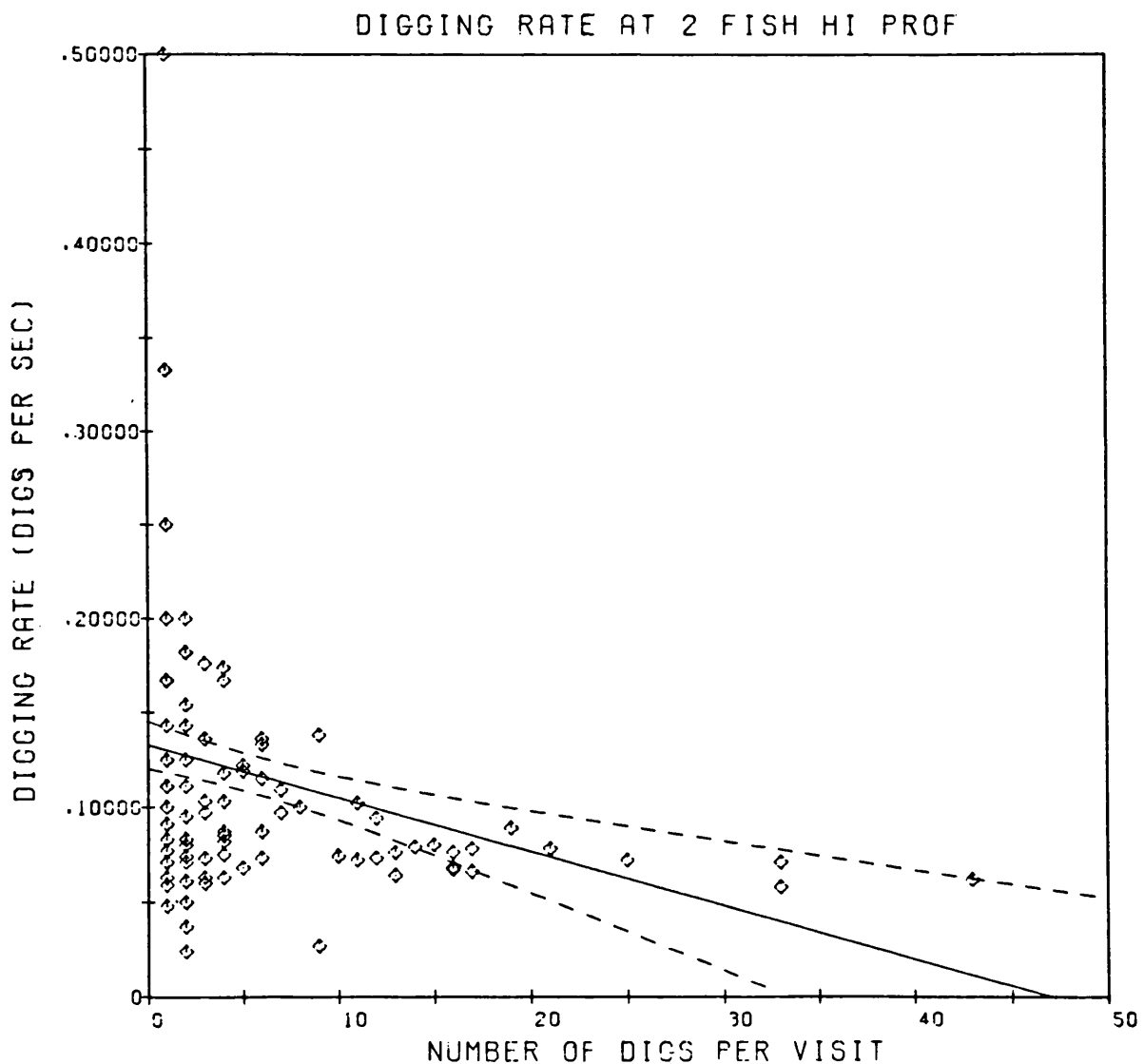


Figure 13 The relationship between digging rate and the number of digs made during a visit, on the low profitability patch at a group size of five. Patches differed in profitability. The regression line and 95% confidence limits are plotted. ($n=184$, $b=-0.007$, $R=0.27$, $F=14.23$, $P<0.0001$).

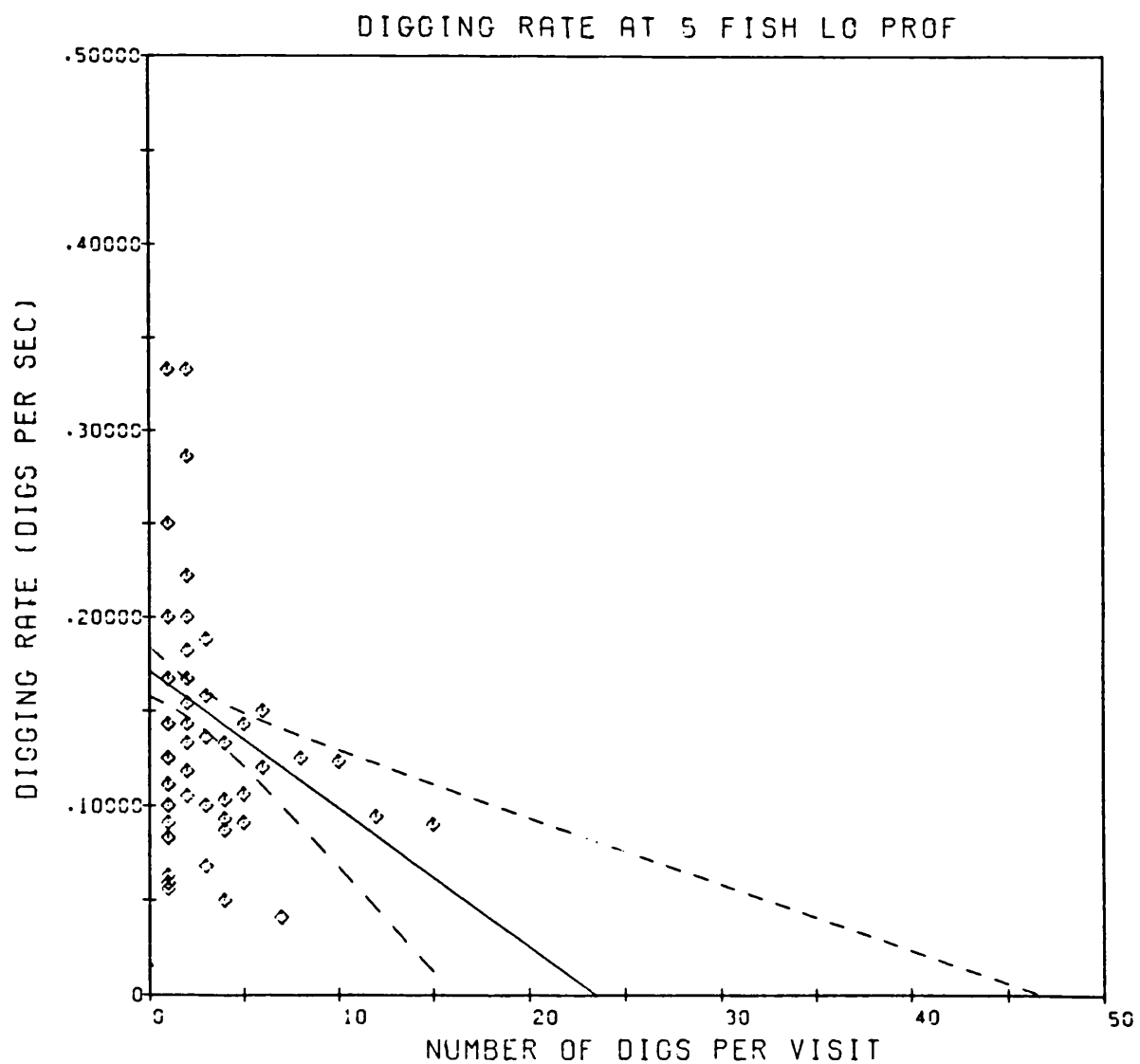
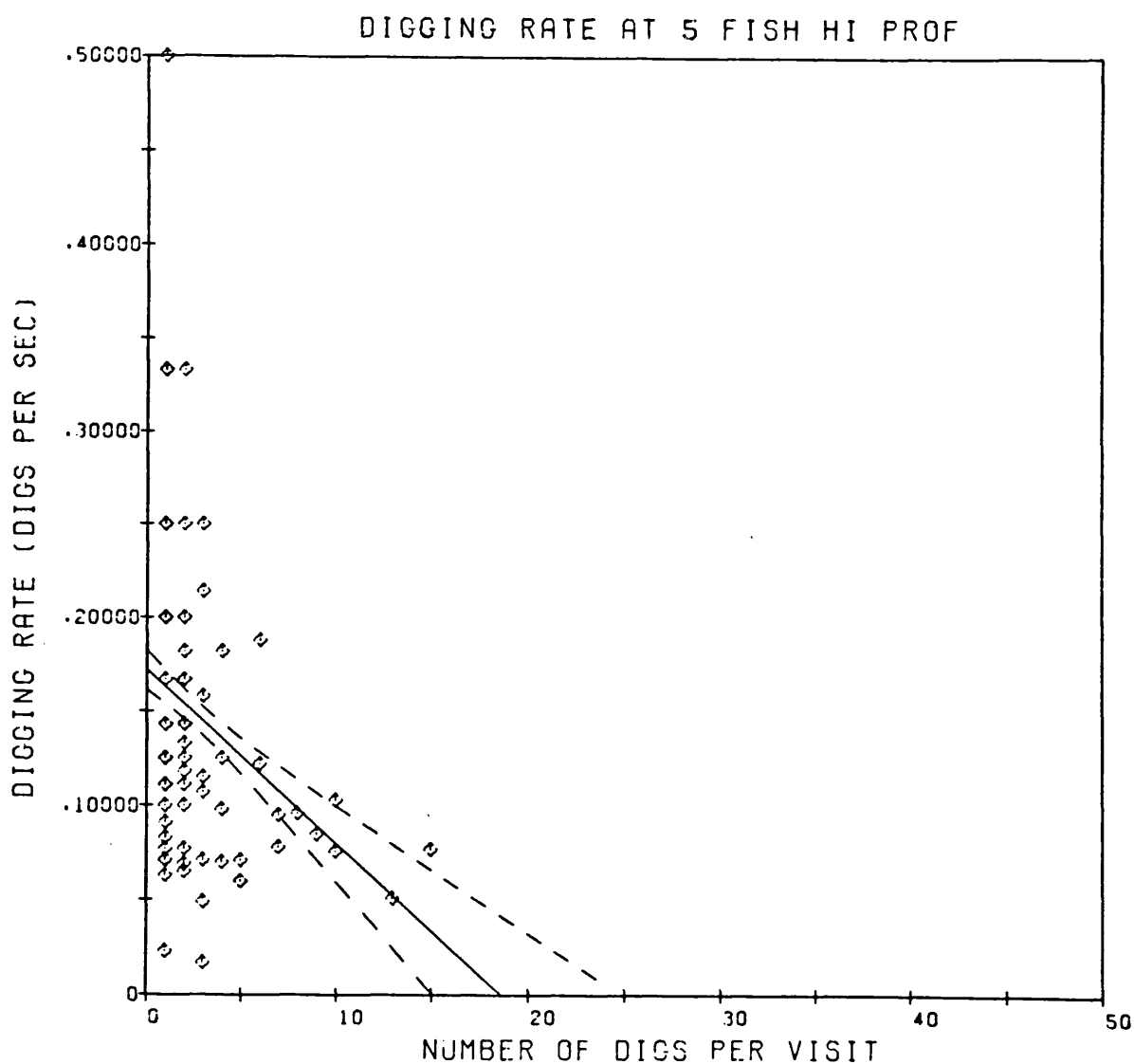


Figure 14 The relationship between digging rate and the number of digs made during a visit, on the high profitability patch at a group size of five. Patches differed in profitability. The regression line and 95% confidence limits are plotted. ($n=473$, $b=-0.009$, $R=0.31$, $F=48.80$, $P<0.0001$).



Possible implications of these results will be discussed in Chapter 6.

4.4 DISCUSSION

This experiment reveals some important differences in the ways in which group size affects a stoneloach's exploitation of two food patches, of either equal or different profitability. When patches of equal profitability were present, a group of five fish made a greater number of shorter visits to them. This increase was not accompanied by a reduction in the number of digs made to obtain food, so it appears that an individual's intake should be similar at both group sizes. However, the increase in the number of visits made to the patches observed at the larger group size may confer an advantage on a member of such a group when searching for prey in an environment of varying patch quality. For example, members of a group of five goldfish were more sensitive to changes in patch profitability than members of a group of two individuals (Pitcher & Magurran 1983).

By making a greater number of shorter visits to the patches, the fish had a greater opportunity to sample the environment. Whether or not the fish actively attempted to sample the environment is unimportant; if a greater number of visits to the patches were made, and more switching between the patches took place, and both patches were visited on a higher proportion of occasions, the fish had a

greater potential for gaining information about the environment. These parameters will therefore be grouped together as an indication of the level of "sampling".

When one patch was four times as profitable as the other, an increase in the total number of patch visits was observed, however it was accompanied by a reduction in the overall number of digs made, so reducing an individual's food-finding opportunities. The number of visits made, to both patches, increased significantly when group size was increased. The visits were of a shorter length, indicated by the reduction in the total amount of time spent on each patch.

The decrease in the overall number of digs was due to a reduction in exploitation of the poorer patch, supporting the hypothesis that larger groups of foragers are more "quality conscious" (eg Pitcher & Magurran 1983). The level of exploitation of the high quality patch remained unchanged when group size increased from two to five individuals.

In their study with goldfish, Pitcher & Magurran (1983) found that fish in a group of two spent less total time foraging than when in a group of five, but that they allocated more of their foraging time to feeding on the best of three different density food patches. At the larger group size, the fish made more sampling visits to the patches. This had the effect of reducing individual intake below the maximum possible, but enabled the fish to

recover their feeding performance much more rapidly after the positions of the different profitability patches had been switched. The fish were found to be feeding further below the optimum predicted by simple foraging theory at the larger, than at the smaller group size.

The result that stoneloach in a group of five made a smaller total number of feeding attempts suggests that they may also have been feeding further below the optimum at the larger group size, although without knowledge of digging efficiency this cannot be stated with any degree of certainty.

Pitcher & Magurran (1983) postulated that their goldfish spent less time foraging when in a group of two as the fish perceived themselves to be at a greater risk from predators, and as a consequence had to devote more of their time to being vigilant. This could explain why the smaller group foraged closer to the predicted optimum, as the smaller proportion of time available for foraging in the smaller group had to be used more efficiently.

However, Milinski & Heller (1978) found that sticklebacks foraged sub-optimally when under a risk of predation. When threatened with a model predator, the fish attacked less dense areas of a swarm of *Daphnia* as these were less confusing to them, and enabled them to be more vigilant. Werner & Mittelbach (1981) found that bluegill sunfish *Lepomis macrochirus* grew at a slower rate when exposed to a

risk of predation, as they spent more time hiding in the weeds.

It is nevertheless possible that the increased sampling by stone loach observed in the larger group size, at both equal and different patch profitabilities, was due to a reduced need for vigilance. Magurran & Pitcher (1983) found that both minnows and goldfish became less timid as group size increased. In a more recent study, Magurran, Oulton & Pitcher (1985) tested the reaction of shoals of foraging minnows to an approaching model pike. Minnows in larger shoals noticed the pike sooner, but left the patch later, than those in smaller shoals, indicating that smaller shoals were less vigilant.

It is adaptive for animals to continue to sample a stable habitat as an "insurance policy" against future changes going unnoticed (Caraco, Martindale & Whittam 1980). In a situation where patches become depleted, sampling will presumably be equally important, if not more so.

When the two patches were equal in profitability, there would presumably have been no tendency for the fish to aggregate on one patch or the other, which could lead to interference between individuals and a consequent reduction in food intake.

When the patches differed in their profitability the level of sampling increased with an increase in group size, as was the case when the patches were equal in profitability.

It is thus possible that at a group size of five, the fish were better able to identify the superior patch and so attempted to exploit this patch to a greater extent. However, a tendency to aggregate on the best patch (eg Goss-Custard 1970a, 1977a,b) can cause competitors to interfere with each other, resulting in a poorer feeding rate (see Chapter 5). This does not mean to imply active aggression, which was not observed in this study, but rather passive interference (eg Sutherland 1983).

Fewer digs were made on the poor patch, so in order to maintain its food intake an individual would have had to feed more on the best patch. If prevented from doing so by the activities of other foragers, the fish would suffer a loss of feeding attempts (digs)(Table 4.2), and possibly, therefore, food intake. No evidence for interference between individuals was found when patches were equal in profitability; the number of digs made during each visit being unaltered by the presence of conspecifics.

Intuitively, the number of individuals attempting to feed on a patch of a given size will determine the level of interference experienced by an animal feeding there. Where patches are equal in profitability, the same number of competitors will be expected on each patch, if they obey an "ideal free" distribution (Fretwell & Lucas 1970, see Chapter 5). The predicted number will therefore be, on average, 2.5. At a profitability ratio of 4:1, four fish will be expected on the best patch, and the larger number of fish is more likely to lead to interference.

To determine whether interference occurred, it is essential to know the number of conspecifics present. Due to the small angle of view of the camera lens, necessary in order to follow the subject fish, the number of other fish on the patch, or in the immediate area, could not be determined very reliably. The possibility of error will be lower when the patches are equal in profitability, as the number of fish present on each of the patches is likely to be lower than the number found on the best patch at the 4:1 ratio. Therefore a similar analysis to that performed for equal patch profitabilities was not considered to be justified.

y?
An increase in group size may have led to a greater feeding efficiency, whereby each dig gave rise to more food. If this were the case, the fish's food intake need not necessarily have been reduced by it making fewer digs. Without this information, the effects of increasing group size on foraging efficiency cannot be determined.

It would be informative to determine the distribution of all the fish over the patches, and to determine more reliably whether interference in the area of the high profitability patch could account for these observations. This hypothesis will be examined in more detail in the following chapter.

CHAPTER 5

EXPERIMENT 3. GROUP SIZE AND THE IDEAL FREE DISTRIBUTION

5.1 INTRODUCTION

5.1.1 The ideal free distribution

Fretwell & Lucas (1970) developed the concept of the ideal free distribution to account for the distribution of breeding birds between available habitats. Parker (1970, 1974) independently proposed a similar argument to explain the distribution of dungflies, *Scatophaga stercoraria*, searching for mates. The term "ideal free" was applied to the concept by Fretwell & Lucas (1970) as all individuals are assumed to be ideal in their ability to judge the suitability (profitability) of the different potential sites, and free to move between sites. In this case, profitability is taken to mean the amount of food which can be obtained on a given site. The theory as originally proposed by Fretwell & Lucas (1970) makes the assumptions that all individuals have an equally good competitive ability, and that all forage in order to maximise their intake rate whilst feeding (Sutherland & Parker 1985).

The original model (Fretwell & Lucas 1970) made the further assumption that reduced habitat quality resulted from an increase in competitor density within habitats. The model was extended to incorporate Allee's principle, and thus

modified predicted that habitat quality should increase as competitor density increased, up to a certain point, and then decline. Due to this effect, small changes in the population may cause erratic alterations in the distribution of species following Allee's principle (Fretwell & Lucas 1970).

Fretwell & Lucas (1970) proposed a second model, the ideal despotic distribution. In this case the assumption is made that individuals differ in their competitive ability, and that some will be able to obtain a disproportionate share of the available resources, either through dominance or territoriality.

5.1.2 Ideal free searching as an ESS

A strategy is an ESS (evolutionarily stable strategy) if, when adopted by most members of the population, it cannot be invaded by the spread of any rare alternative strategy (Maynard Smith 1972, 1982). An ESS can be one of two basic types. The first is a pure ESS where, for example, in condition c play the unique strategy A . The second is a mixed ESS where, for example, in condition c play pure strategy A with a probability (P) of P_A , B with probability P_B , C with probability P_C and so on; the values of P_A , P_B , P_C etc being prescribed by the ESS (Parker 1984).

Ideal free searching is an example of a mixed ESS (eg Parker 1978, Milinski 1979, Maynard Smith 1982, Parker 1984). The best choice of habitat will always depend on

what other individuals are doing (Pulliam & Caraco 1984) and therefore can be modelled as an alternative-option scramble (Parker 1984). When all individuals are distributed in accordance with the ideal free distribution, and as long as all other individuals remain in the same place, no individual can benefit from moving elsewhere (Pulliam & Caraco 1984, Parker 1985). This assumes that, at equilibrium, all individuals have the same fitness, as in the original model of Fretwell & Lucas (1970) and Fretwell (1972).

Parker (1984) describes two extreme examples of the ideal free distribution as an ESS. The first of these (Type 1 (Parker 1984)) is where resources deplete as they are exploited; renewal of resources does not occur. The model proposed by Fretwell & Lucas (1970) is essentially of this type (Parker 1984). A series of equally-sized patches in a habitat are ordered in accordance with decreasing profitability, where profitability is a function of prey density; the best patch providing the highest rate of prey capture. So long as there is no interference between competitors (see section 5.1.3) all competitors should first exploit the best patch, with the highest prey density. Once this patch has been depleted to a prey density equal to that of the second best, the competitors should divide themselves equally between both patches. These should then be depleted simultaneously until the prey density of the next best patch is reached, when the competitors should divide themselves equally over all three patches, and so on. The ESS consists of continually

keeping the rate of gain constant for all competitors as individuals move onto new patches as existing ones become depleted (Parker 1984).

The second situation (Type 2 (Parker 1984)) is where resources are continually being renewed and depletion does not occur. The rate of input of resources varies between patches, the best patch having the highest input rate. The ESS consists of a division of the competitors between the patches in accordance with the input matching rule (Parker 1978, 1984). For example, in a situation where there are two patches, one providing resource items at twice the rate of the other, twice as many competitors should go to the better patch. It seems likely that, in natural systems, a combination of the two extremes would occur (Parker 1984). However, experimental tests of the ideal free distribution have concentrated largely on systems of the second type, where there was continuous resource renewal (eg Davies & Halliday 1979, Milinski 1979, 1984, Harper 1982).

5.1.3 Aggregation and interference

When there is no interference between predators, resulting in a decrease in foraging efficiency, the instantaneous rate of prey capture depends solely upon the prey density, and is independent of the number of competitors on the patch (Parker 1984). However, when interference between competitors occurs, the amount of food which a predator can obtain in a site depends upon two factors; the density of food, and the level of interference experienced due to the

presence of other predators (eg Sutherland 1983). It follows therefore, that if the ideal free distribution is obeyed, the predators should distribute themselves so that the effects of food abundance and interference balance out, and all achieve a similar feeding rate. If one site enables a better feeding rate than the others, more predators should move there, leading to an increase in the level of interference experienced, which, in turn, eventually removes the difference between the sites so that the feeding rate returns to uniformity (Sutherland 1983, Sutherland & Parker 1985).

There is a considerable body of evidence that predators aggregate in areas of high prey density. For example, some wading birds aggregate where food is most dense, however this tendency is limited by an increase in interference at higher bird densities (Goss-Custard 1970a, 1977a,b, O'Connor & Brown 1977, Bryant 1979). The number of aggressive encounters between oystercatchers *Haematopus ostralegus* over food items and feeding sites increased with a rise in predator density, resulting in a loss of feeding opportunities (Goss-Custard 1977b). Waders detecting food by sight were adversely affected by interference and fed spaced widely apart, while those detecting food by touch were not affected and fed close together (Goss-Custard 1970b, 1976). In the case of redshank, *Tringa totanus*, when feeding by sight on *Corophium* the birds were dispersed, and when feeding by touch on *Hydrobia* the birds fed together in a flock.

5.1.4 Evidence for the ideal free distribution

Evidence in support of the predictions of the ideal free distribution has been obtained from several species. Milinski (1979) found that sticklebacks feeding on two simulated drift food patches of *Daphnia magna* distributed themselves between the patches in the ratio of patch profitabilities. In a subsequent study, Milinski (1984) accurately measured each fish's food intake, and found consistent differences between individuals. Under these conditions the ideal free distribution will therefore be inappropriate.

However, a modification of Harley's (1981) Relative Payoff Sum (RPS) learning rule by Regelman (1984), which allowed for unequal competitive abilities, and also for variations in travel time, was able to account for the observed distribution. The modified RPS rule predicted that the fish would distribute themselves in accordance with the patch profitability ratio, but that good competitors would distribute themselves more rapidly. The distribution of the poor competitors, which would take longer to distribute themselves, will therefore be affected by the distribution of the good competitors in addition to the profitability of the patches. The model also made the prediction that increased travel costs would decrease the amount of switching between patches. The predictions of the modified RPS learning rule were broadly met in Milinski's (1984) experimental study.

From Milinski's (1979, 1984) studies it is apparent that although results may superficially fit an ideal free distribution, in reality differential competitive ability can result in individuals obtaining different amounts of the resource in question.

Fraser & Sise (1980) examined the distribution of stream minnows *Semotilus atromaculatus* and *Rhinichthys atratulus* between 11 pools in a natural stream, connected by riffle areas, and obtained results consistent with the predictions of an ideal free distribution.

In a study of male toads *Bufo bufo* competing for females in and around a mating site, Davies & Halliday (1979) found that the males were distributed in the two areas (either in the pond, or in the surrounding area) in a way compatible with a model assuming that the unpaired males distribute themselves so that there is a spatial ESS. In this way, an individual male had an equal chance of finding a female whether he was actually in the pond, or in the surrounding area. This study was similar to Parker's (1970, 1974, 1978) examination of mating in the dungfly *Scatophaga stercoraria*, where males searching for females, either on cowpats or in the surrounding grass, were distributed as predicted by a spatial ESS.

Harper (1982) fed mallard ducks *Anas platyrhynchos* with pieces of bread thrown in at different frequencies from two different places on the edge of a pond. The ducks quickly distributed themselves as predicted by the ideal free

model. However, some birds were much better competitors than others and so obtained a disproportionately large share of the food, thereby violating an assumption behind the ideal free model, namely that all competitors must have an equal competitive ability. Harper (1982) suggested that other ducks could respond to the number of despots by the resulting decrease in food availability, and correct their assessment of patch profitability by taking into account the positions of the dominant birds.

Whitham (1980) studied the colonisation of leaves of the narrowleaf cottonwood *Populus angustifolia* by gall-producing aphids *Pemphigus betae*. Stem mothers emerging from overwintering found an immature cottonwood leaf, where their feeding gave rise to a hollow gall, within which the female aphid produced as many as 275 young (Whitham 1980). Each leaf could be considered as a patch, and as large leaves offered a better habitat, selection pressure would have favoured stem mothers which colonised these leaves. Once all the best leaves had been occupied, newly-arriving stem mothers could either settle on a large leaf where there was already a stem mother, or settle on a smaller but inferior leaf, where no stem mother was present. Whitham (1980) found that larger leaves were able to support more galls, the overall distribution of galls being consistent with the prediction of the ideal free model.

It was observed that individuals in different patches had the same average fitness, but also that fitness varied

greatly according to the aphid's position on the leaf. On leaves with more than one gall, the stem mother nearest the base of the leaf had a greater reproductive success. This position was vigorously defended during the period prior to gall formation (Whitham 1979). During this period, newly-arriving stem mothers sometimes competed with established individuals and displaced them from the superior basal position. Once gall formation had occurred the aphids became separated by host tissue, and behavioural interactions ceased (Whitham 1980).

The patches were therefore highly heterogeneous, which violated a further assumption of both the ideal free and ideal despotic (Fretwell & Lucas 1970) models, which stipulates that patches must be homogeneous in their suitability to competitors. As in Harper's (1982) study, the observed distribution was compatible with that predicted by the ideal free model when the distribution between patches was considered, but the share of the resource varied between individuals within each patch.

A similar result was obtained by Godin & Keenleyside (1984) who studied the way in which groups of flag cichlids *Aequidens curviceps* distributed themselves between two drift food patches of live fish fry, at three different patch profitability ratios. The observed distribution closely approximated that predicted by the ideal free distribution at ratios of 1:1 and 2:1. However, at a ratio of 5:1, more fish than predicted were found in the less profitable patch. On average, individuals received equal

amounts of food at ratios of 1:1 and 2:1, again as predicted, but at 5:1 a higher feeding rate was observed in the better patch. It was found that some fish in each patch obtained more food than others, this was however not attributable to differences in social rank. Godin & Keenleyside (1984) postulated that individual differences in intake may have been due to differing abilities to assess patch profitabilities quickly and accurately, and also to respond to and attack prey first.

Clarke (unpublished data) studied the distribution of groups of *Tilapia zilli* between two patches, where individuals differed widely in competitive ability. As expected, dominant individuals obtained a disproportionately large share of the food. This was achieved by positioning themselves below the point of input, and excluding other fish. The most dominant individual generally stationed itself in the best patch, the second most dominant fish positioning itself in the other patch. Using this tactic, the latter individual was able to obtain a higher intake than was achievable by competing with the most dominant fish for food on the best patch.

5.2 METHODS

The basic methods used in this experiment were as outlined in Chapter 2. Two group sizes were used, 6 and 12 fish, and the distribution of the individuals between two patches with profitability ratios of 1:1, 2:1 or 5:1 recorded.

Five replicate groups of fish were tested, and 10 replicates obtained from each group for each experimental condition. A new set of experimental fish was used for each patch profitability ratio, to avoid the re-use of experienced animals.

Before recording a set of replicates of 10 days duration, the fish were acclimatised to the experimental protocol for between 7 and 10 days. As the distribution of the whole group was the subject of investigation, and not just the behaviour of a particular fish within the group, as in Experiments 1A, 1B and 2, no marked subject fish was needed. The distribution of a group of 6 fish was studied first, then further fish were added to produce a group of 12, the distribution of which was examined after an acclimatisation period. The behaviour of new and established group members could not be distinguished after this period.

The experimental aquaria were set up as shown in Figure 1. The order in which patches were introduced was alternated, as was the location of the two different profitability patches (in the case of ratios of 2:1 and 5:1). The order of recording the five groups was randomised, to eliminate possible effects of the length of time since dimming the lights.

Patches were set up as described in section 2.5. 0.2g of food (tubificid worms) per fish was used, the total being divided between the patches to produce the required

profitability ratio.

The distribution of fish was recorded by positioning a video camera fitted with a 8.5mm wide angle lens vertically above the experimental tanks. A rotatable polarising filter was used to reduce reflection from the water's surface. The IR light source was positioned at 45° to the angle of the camera. Possible effects of greater illumination at one end were controlled for in the protocol, by alternating the order of patch introduction and the location of the high profitability patch (where applicable).

The five experimental aquaria were arranged side by side on the floor, with the video camera and IR light source fixed to a moveable trolley which could be moved along to film from each tank in turn. This system enabled a day's trials to be recorded in quick succession, and with the minimum of disturbance to the fish. The tanks were positioned on sheets of 25mm particleboard, to offer a degree of isolation from floor-borne vibrations.

Each trial lasted for 15min, after which patches were left in place for 4h, to give the fish an opportunity to consume all of the food available.

The video recordings of the trials were subsequently analysed, and the distribution of the fish over the aquarium floor recorded, at 10sec intervals. The fish were recorded as being in either of the two feeding areas at the

ends of the tank, or in the central, non-feeding, area (see Figure 1).

5.3 RESULTS

5.3.1 Group size, patch profitability ratio and stone loach distribution.

In previous studies of the ideal free distribution, where groups of fish foraged on patchily distributed prey (eg Milinski 1979, 1984, Godin & Keenleyside 1984), the foraging area was considered as consisting simply of two halves. Each contained a food patch of either equal or different profitability. The relative profitability of the two patches was then used in order to predict the ideal free distribution. For example, at a profitability ratio of 2:1 a group of 6 competitors would be expected to divide themselves so that there were four individuals on the best patch, and two on the other.

However, in this experiment the group of fish did not simply divide themselves into the two halves of the tank. As expected, a group was found around each patch, but there were also a number of individuals in the central area of the tank, where no food was present. Observations of video recordings made whilst analysing the trials suggested that the latter individuals were not merely travelling between the patches, but rather remaining in the central area for an extended period. Unfortunately it was not possible to monitor the movements of each individual throughout the

course of each 15min trial, due to limitations to the definition of the video recordings. This would have made it possible to determine the length of time spent by each individual in each part of the tank, and also whether individuals apportioned their time differently.

Figure 1 shows that the patches were located towards the ends of the tank, so that a distinct central region was present. This will inevitably have had an effect on the distribution observed, but this does not reduce the validity of the result, which simply reflects the fishes' decisions in a given environment. Bearing these points in mind, the position of each fish was recorded as being in either one or the other of the two areas containing the patches, or in the central area (see Figure 1). The distribution of the fish over 15min (900sec) from the introduction of food is shown in Figure 15 (A-F), for each group size and profitability ratio.

5.3.1.1 Ratio of fish between patches

If a group of competitors divides as predicted by the ideal free distribution, the ratio between the number of individuals in each patch area will match that of patch profitability. In order to test whether this was the case, the effect of the individuals in the central area was removed, by calculating the ratio between the number of fish in the two patch areas, and ignoring those in the centre. The results are shown in Figures 16 and 17, for group sizes of 6 and 12 respectively.

Figure 15. (Parts A - F on following pages).

The distribution of fish over the three areas of the aquarium, given as mean and + or - S.E.

Figure 15 (A) Distribution of fish at group size of 6 and profitability ratio of 1:1

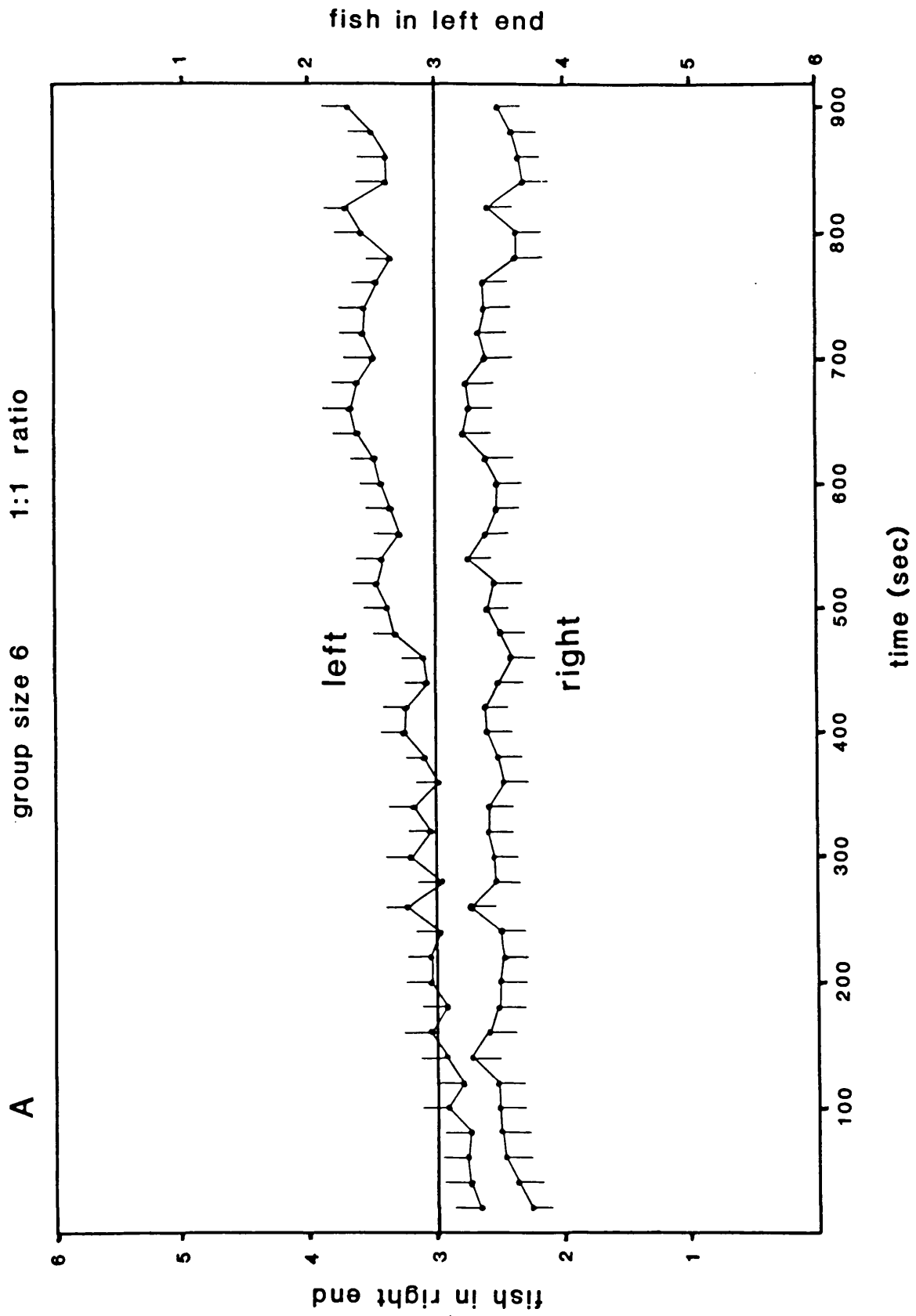
Figure 15 (B) Distribution of fish at group size of 12 and profitability ratio of 1:1

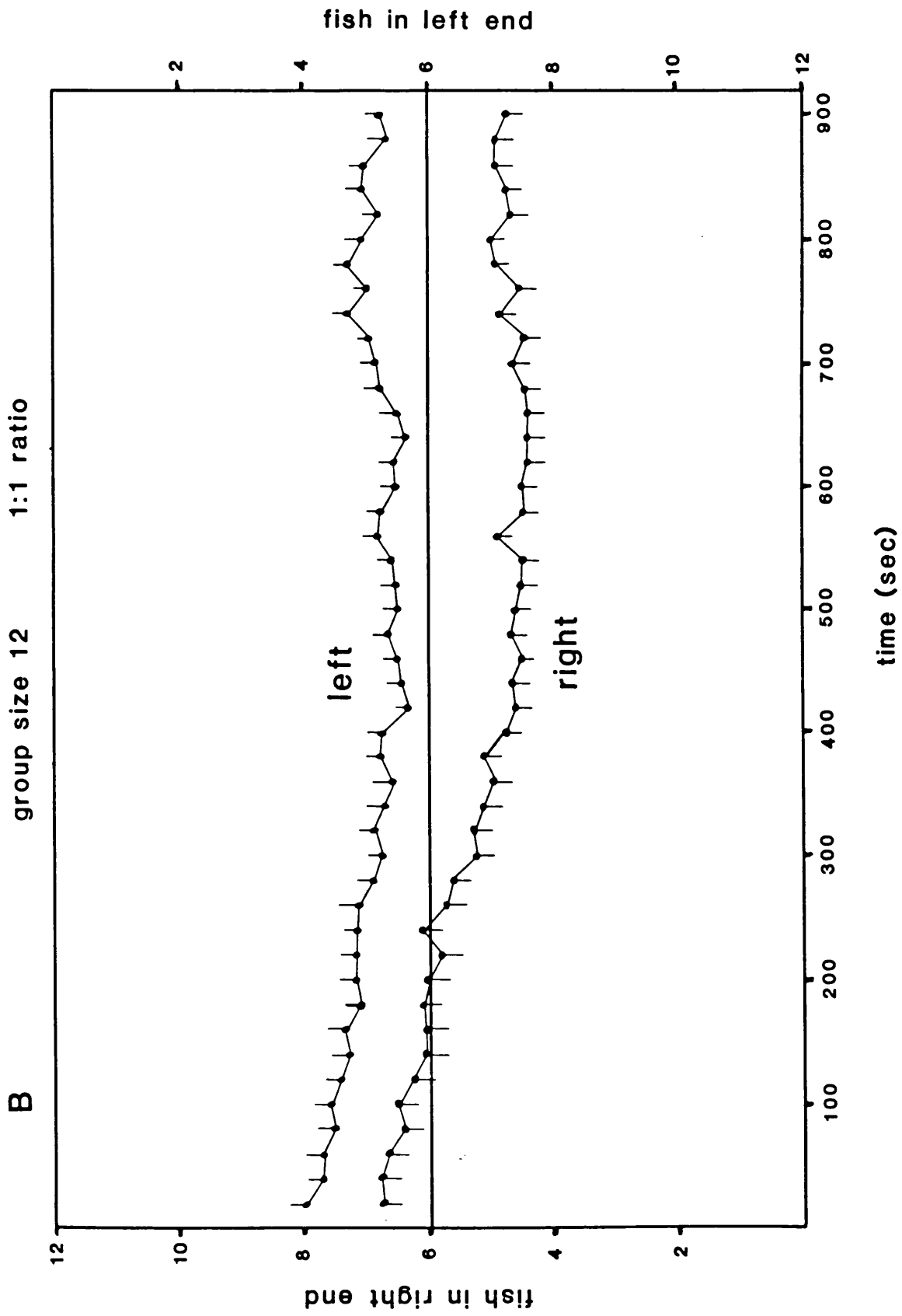
Figure 15 (C) Distribution of fish at group size of 6 and profitability ratio of 2:1

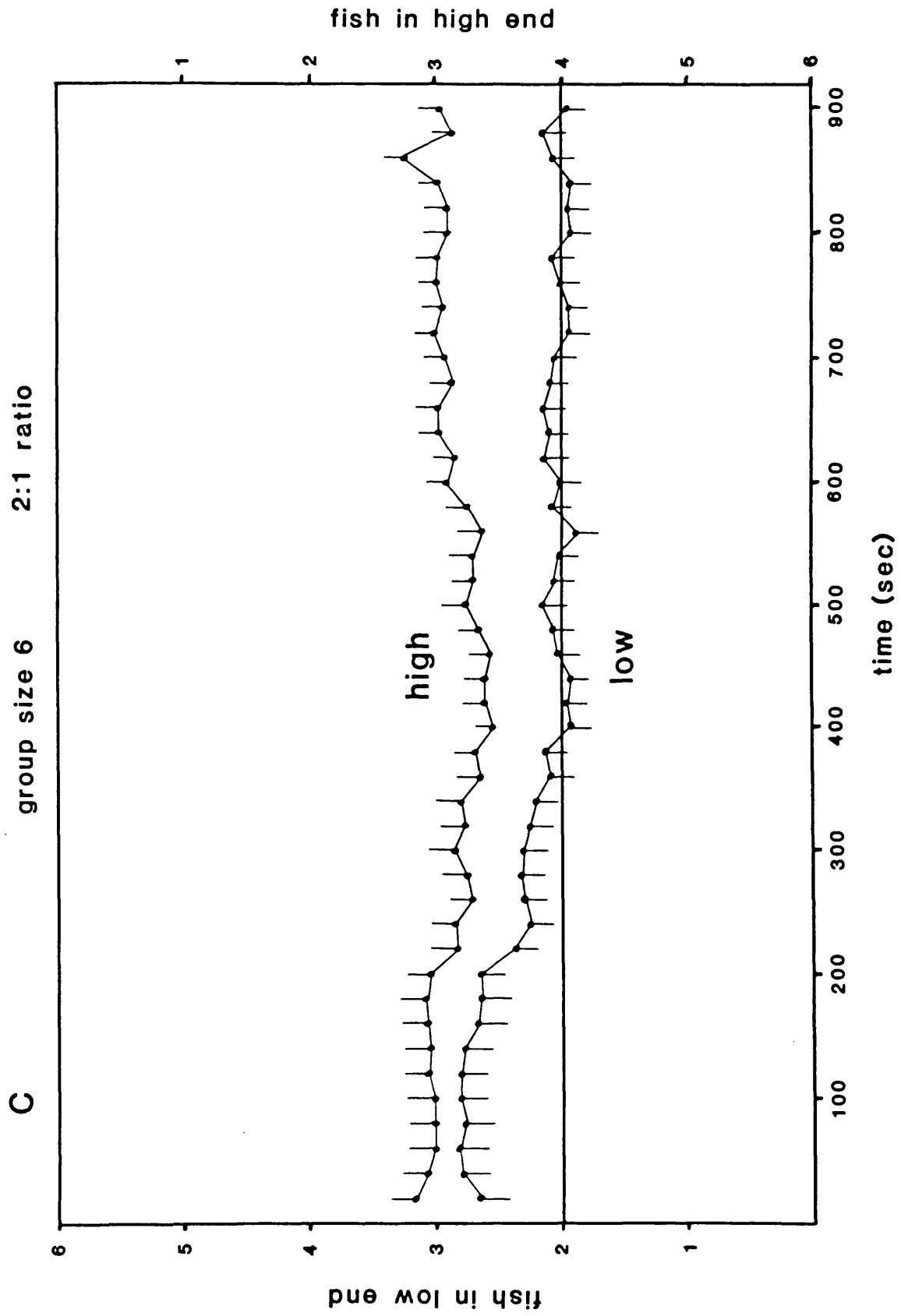
Figure 15 (D) Distribution of fish at group size of 12 and profitability ratio of 2:1

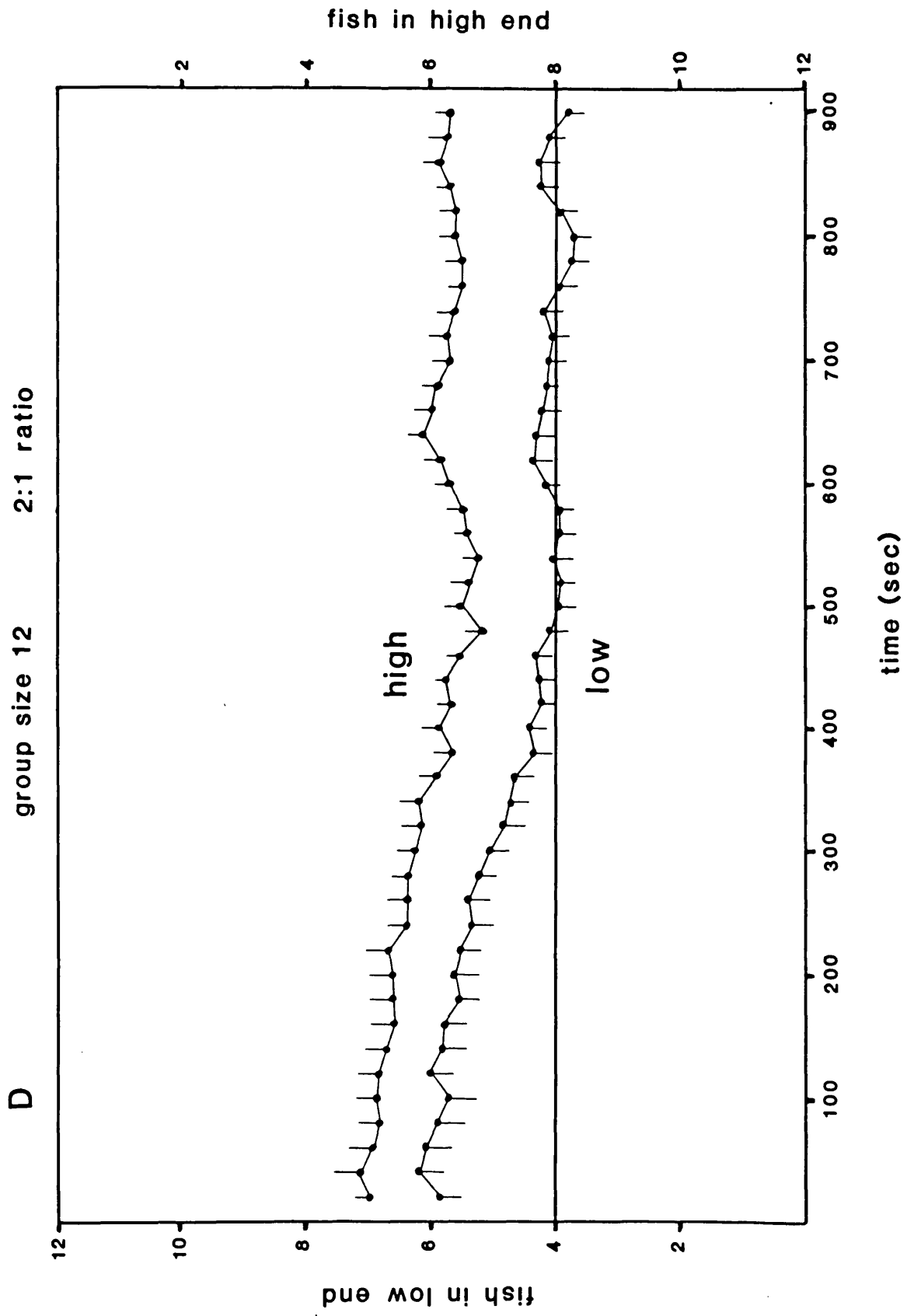
Figure 15 (E) Distribution of fish at group size of 6 and profitability ratio of 5:1

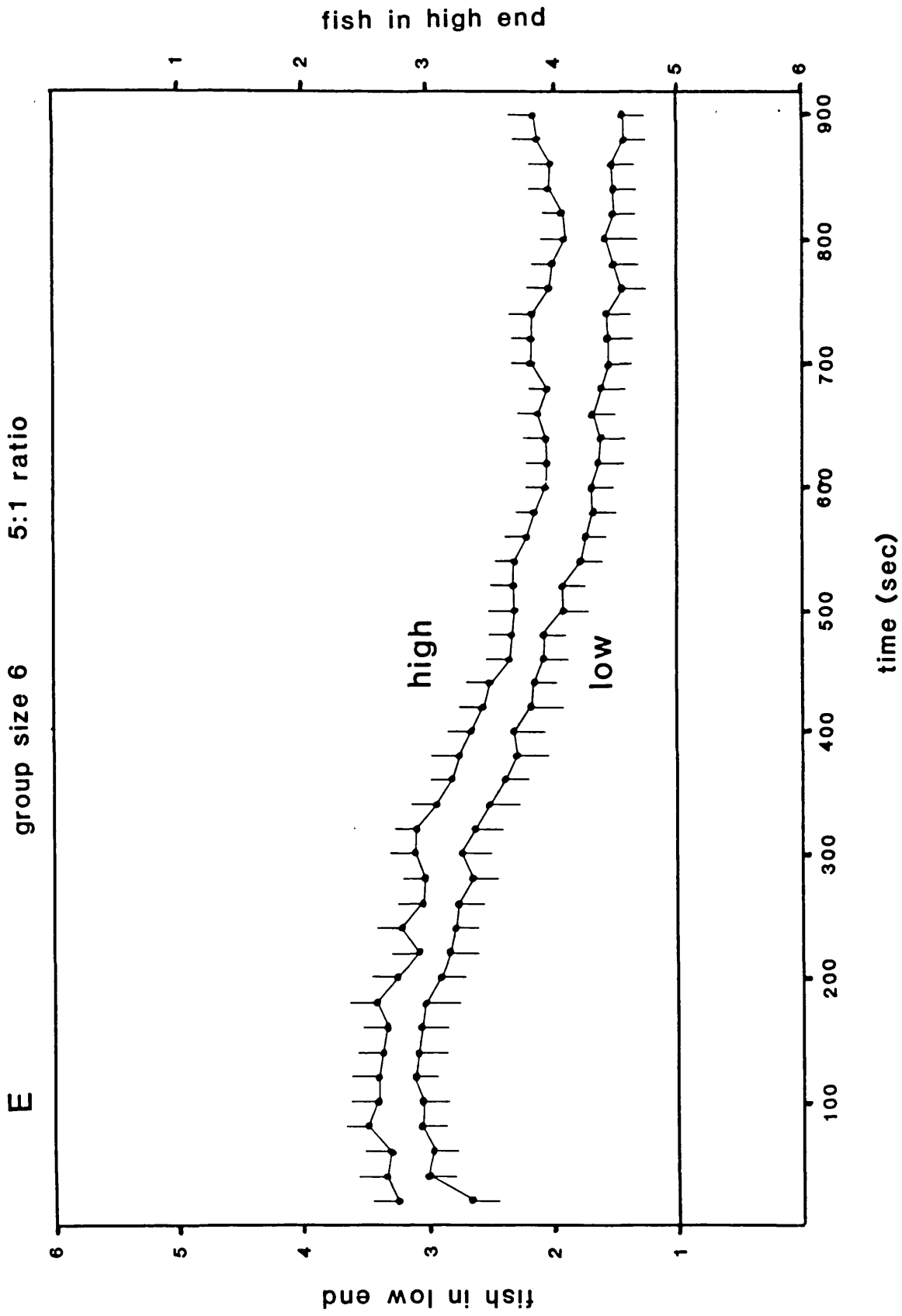
Figure 15 (F) Distribution of fish at group size of 12 and profitability ratio of 5:1











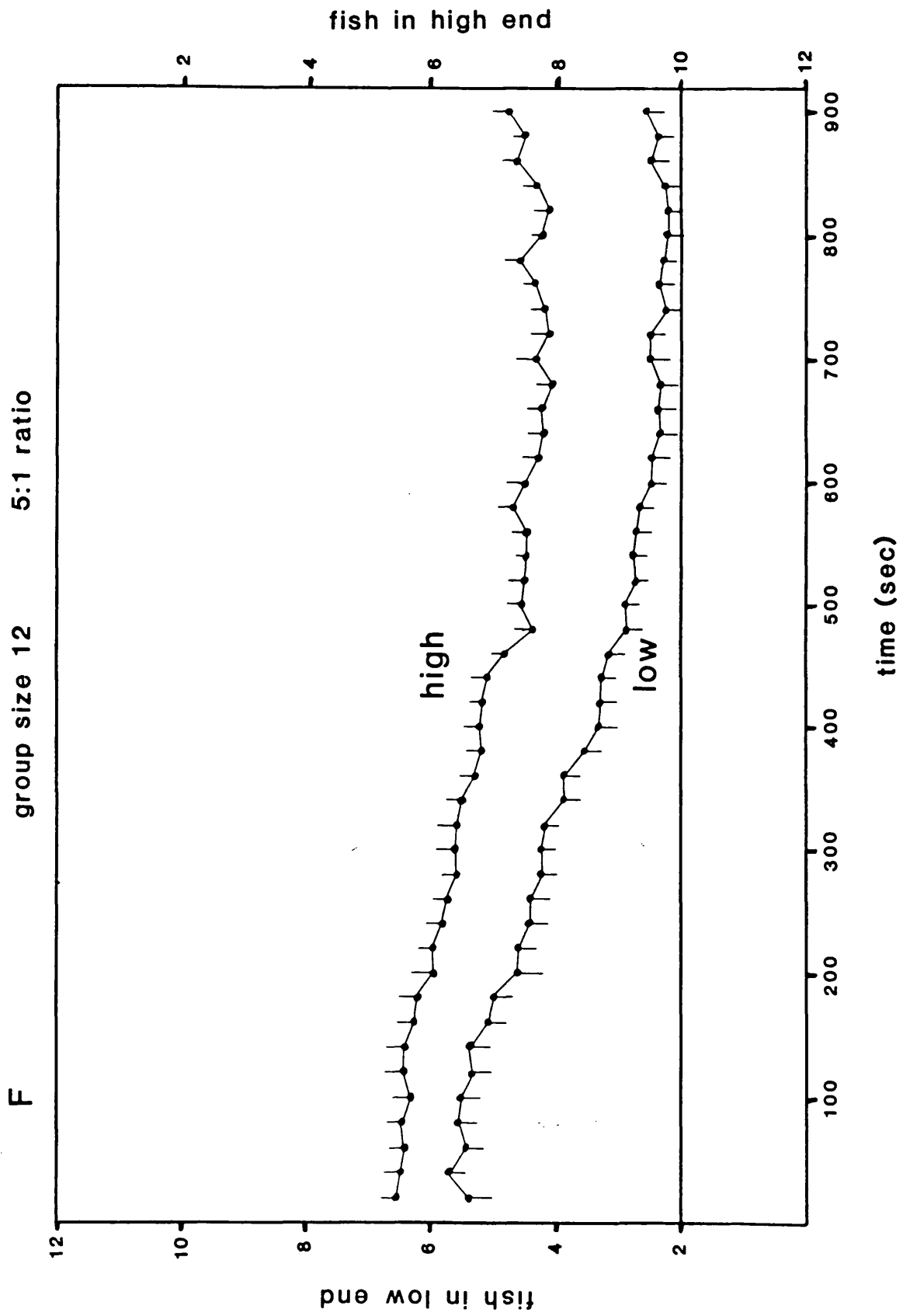


Figure 16 Distribution of fish between feeding areas, expressed as the mean ratio between the number of fish in the high profitability (or left hand) area, and the number in the low profitability (or right hand) area, at a group size of 6. Presentation of the results in this way removes the effect of the presence of fish in the central area of the tank. The ratios shown alongside the right hand Y-axis refer to patch profitability.

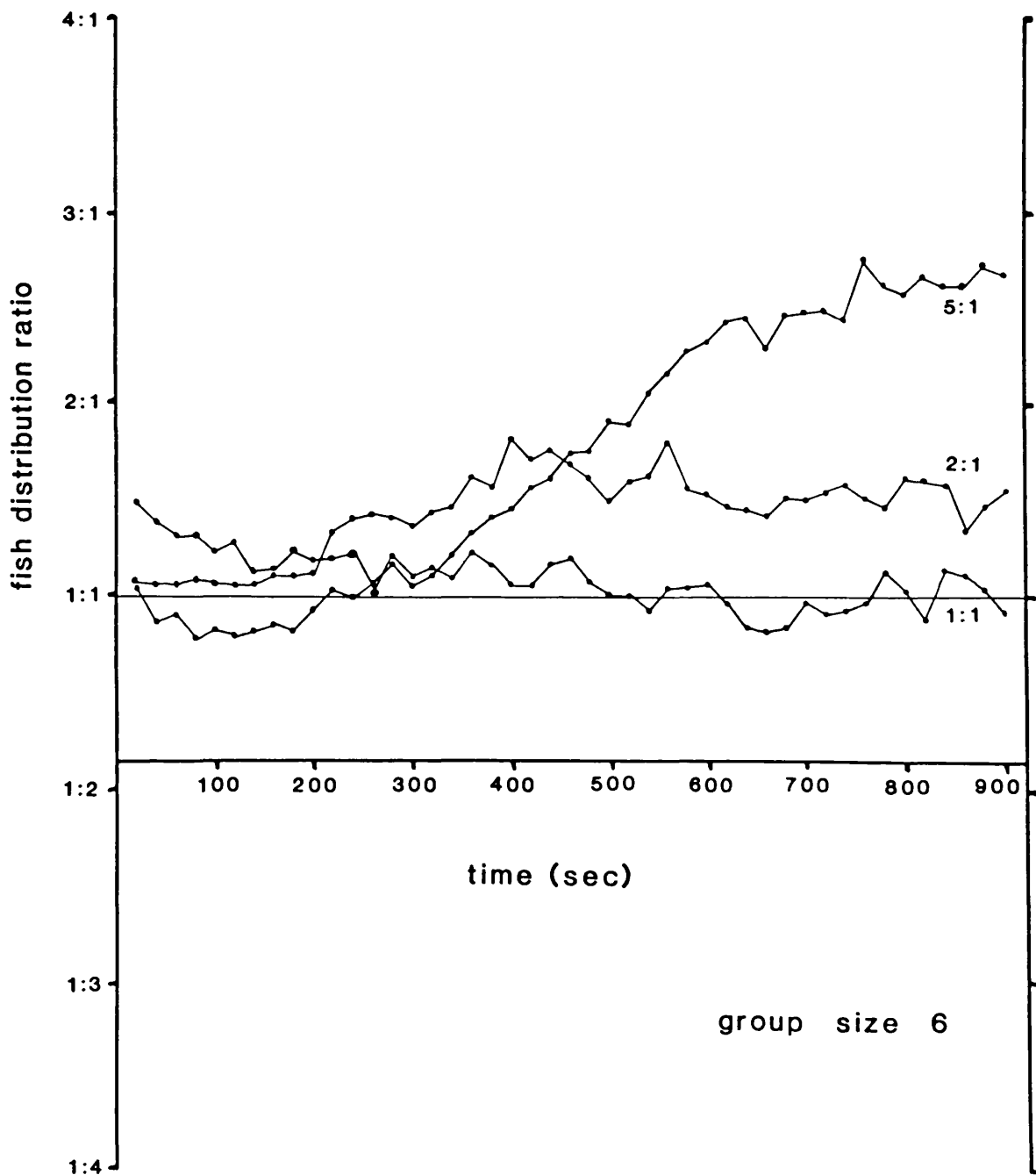
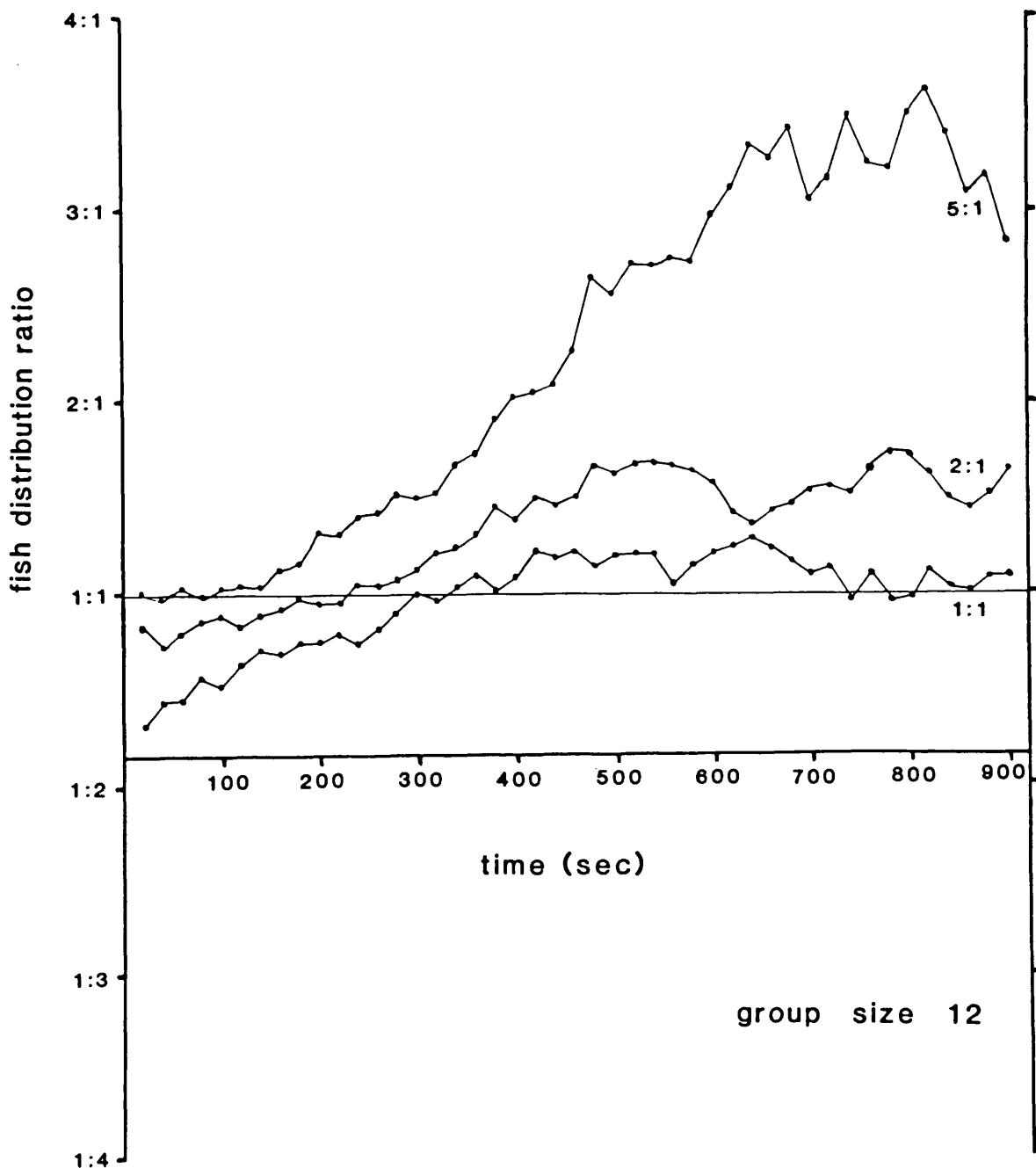


Figure 17 Distribution of fish between feeding areas, expressed as the mean ratio between the number of fish in the high profitability (or left hand) area, and the number in the low profitability (or right hand) area, at a group size of 12. Presentation of the results in this way removes the effect of the presence of fish in the central area of the tank. The ratios shown alongside the right hand Y-axis refer to patch profitability.



When the patches were of equal profitability (1:1) the fish divided themselves in roughly equal numbers between the two areas. When the patches differed in their profitability (ratios of 2:1 and 5:1), the fish adjusted their distribution towards the predicted ratios. At a group size of 6, profitability ratios of 2:1 and 5:1 resulted in distribution ratios of approximately 1.5:1 and 2.7:1 respectively, and at a group size of 12 distribution ratios of roughly 1.5:1 and 3.5:1.

5.3.1.2 Distribution of fish over the foraging area

As shown above, the ratio between the number of fish in each of the two areas of the tank providing a food supply was below that predicted at patch profitability ratios of 2:1 and 5:1 and group sizes of both 6 and 12 individuals. There are two possible explanations; firstly, a greater than predicted number of fish may have been located in the area containing the poorer patch, and secondly, a smaller than predicted number of fish may have been located in the area which contained the better patch. To determine which was the case, or whether a combination of the two possibilities occurred, the distribution of the whole group must be considered, including those individuals situated in the centre of the tank. The distribution is given in Figure 15 (A-F), for each group size and patch profitability ratio.

In all cases, an appreciable proportion of the group was

found in the central area, the proportion increasing with group size at patch profitability ratios of both 1:1 (mean for groups of 6 = 0.12, mean for groups of 12 = 0.14, $n=4500$, $P<0.001$, t-test) and 5:1 (mean for groups of 6 = 0.07, mean for groups of 12 = 0.14, $n=4500$, $P<0.001$, t-test). However, no change occurred at the patch profitability ratio of 2:1 (mean = 0.11 at both group sizes).

The observed number of fish in each feeding area (ie in one of the two end areas, each of which contained a food patch) was tested against that predicted from the ratio of patch profitability, by means of G-tests (Sokal & Rohlf 1981). Observation of Figure 15 (A-F) revealed that a relatively stable distribution of fish was present for approximately the last one third of the 900sec trial duration. Therefore, the distribution over this 300sec period was taken to be the equilibrium distribution, and compared with that predicted. Results of G-tests are given in Table 5.1.

At a group size of 6, and a patch profitability ratio of 1:1, the fish were distributed as predicted. The number of individuals did not differ significantly from the predicted value of three, indicating that the presence of individuals in the central part of the tank had no effect on the overall distribution. For profitability ratios of 2:1 and 5:1, again at a group size of 6, the number of fish in the poor feeding area was as predicted. However, the number of fish in the good area was significantly lower.

At a group size of 12 individuals, results were slightly

Group size	Profitability ratio	Feeding area	G-value	P
6	1:1	LEFT	14.98	NS
		RIGHT	13.25	NS
	2:1	HIGH	26.39	*
		LOW	0.94	NS
	5:1	HIGH	30.11	*
		LOW	21.85	NS
12	1:1	LEFT	24.67	NS
		RIGHT	37.30	**
	2:1	HIGH	48.75	***
		LOW	3.23	NS
	5:1	HIGH	64.83	***
		LOW	13.12	NS

Table 5.1 Results of G-tests between observed and predicted numbers of individuals in each feeding area. In all cases, a significant value of G indicates that there were fewer fish than predicted in the area. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS= not significant.

different. At patch profitability ratios of 2:1 and 5:1, the observed distributions were like those at a group size of 6, in that the number of fish in the poorer area was as predicted, whilst the number in the good feeding area was significantly lower than the predicted value. When both feeding areas were equally profitable (ratio of 1:1), significantly fewer individuals were found in the right hand end ($P < 0.005$, G-test). The number of fish found in the left hand end was not significantly lower than predicted, however the calculated value of G of 24.67 is only fractionally below the value of G of 24.99 which would indicate a significant difference at the 5% level (Rohlf & Sokal 1981).

When the patches were equal in profitability, fish in a group of 6 individuals distributed themselves in the predicted way, whilst at a group size of 12, one feeding area contained significantly fewer fish than predicted. These results suggest that the failure of the ideal free distribution to correctly predict the number of fish found in both high and low profitability feeding areas is a result of competition between conspecifics, and that the fish found in the central area were the result of "overspill" from the high profitability feeding area.

5.3.2 Movements between feeding and non-feeding areas

As noted in section 5.3.1, observations of video recordings of the trials suggested that the individuals in the centre of the tank were not merely those travelling between

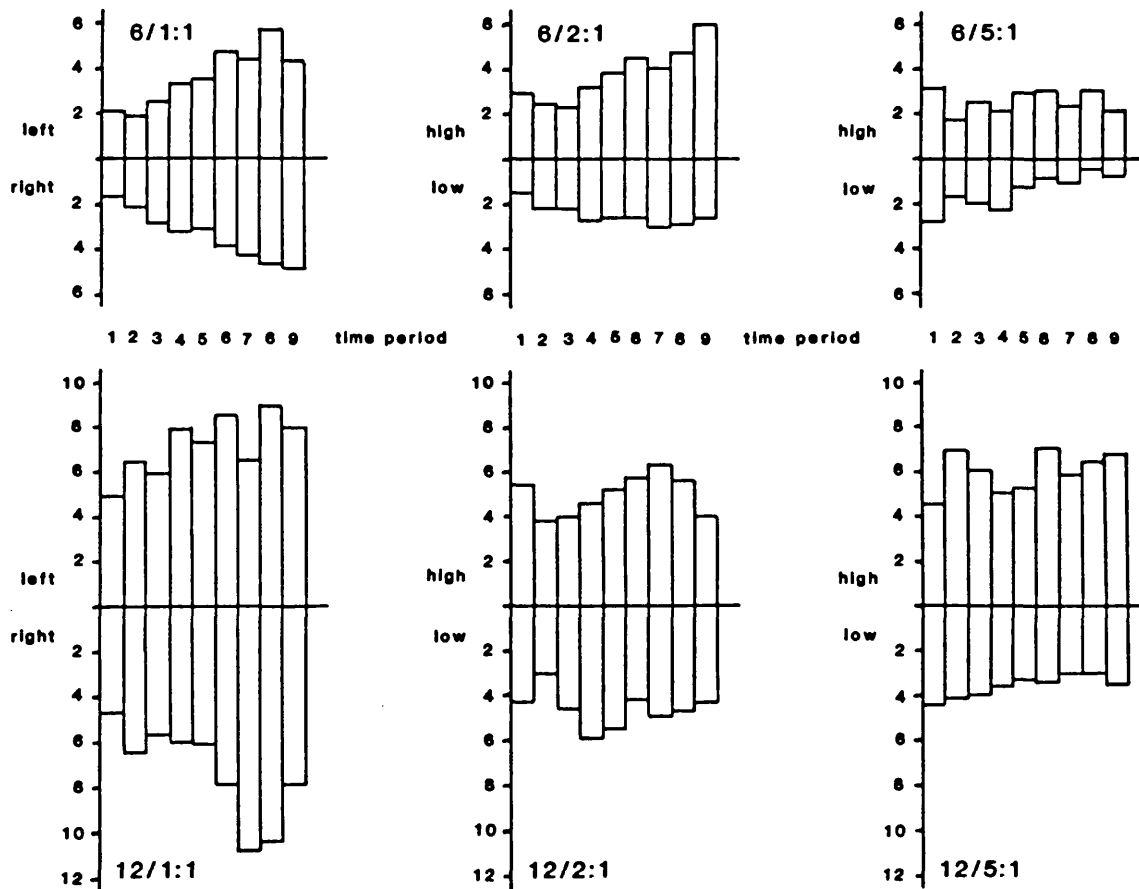
patches, but rather that they were remaining there for an appreciable period of time. The results given in section 5.3.1.2 indicate that the individuals in the centre were the result of overspill from the high profitability area (when patch profitabilities were not equal). To examine this hypothesis further, the movements between each feeding area and the central area were examined.

A subsample of 10 trials (trials 1 and 6 out of 10 replicates for each of 5 tanks) was taken at each group size and patch profitability ratio. The 900sec trial was divided into 9 intervals each of 100sec, and the total number of movements (transfers) in and out of each feeding area in each 100sec period recorded. Results are given in Figure 18.

2-way ANOVA (Hull & Nie 1981) was used to determine the effect of the ratio between patch profitabilities on the number of transfers between each feeding area and the central area (Table 5.2). At both group sizes, a shift in profitability ratio from equality resulted in a significant decrease in the number of transfers between both high and low profitability feeding areas and the central, non-feeding, area.

From Figure 18 it is apparent that in some cases the number of transfers in each time period changes with the length of time since the introduction of food. Linear regression (Hull & Nie 1981) was performed to determine whether there was a relationship between the number of transfers per

Figure 18 Mean number of transfers between each feeding area and the central area, in each of 9 100sec periods. The number of transfers shown includes those both in to, and out of, the central area, for each of the two feeding areas of the tank. Data are given for both group sizes and each patch profitability ratio.



Profitability ratio			Effect of:					
			Ratio		Time		Inter.	
1:1	2:1	5:1						
			F	P	F	P	F	P
6 FISH								
HI	3.59 (2.89)	3.73 (2.59)	2.39 (2.16)	7.93 ***	2.96 **		1.18	NS
LO	3.46 (2.82)	2.49 (2.19)	1.51 (1.83)	16.25 ***	0.54 NS		1.65	NS
12 FISH								
HI	7.16 (3.19)	4.96 (3.37)	5.94 (3.27)	10.19 ***	1.39 NS		0.87	NS
LO	7.31 (3.81)	4.59 (3.34)	3.60 (2.44)	33.73 ***	1.11 NS		2.12	**

Table 5.2 Results of 2-way ANOVA on the effects of patch profitability ratio and elapsed time on the mean number of transfers per 100sec between each feeding area and the central non-feeding area. Results are given as mean and standard deviation (in parentheses). In the case of a 1:1 ratio HI=left, LO=right. *** $P < 0.001$, ** $P < 0.01$, NS= not significant.

100sec, and elapsed time. A regression analysis was performed for each feeding area at each group size and patch profitability ratio (Table 5.3).

At a group size of 6, and a profitability ratio of 1:1, the number of transfers per 100sec increased with elapsed time for both feeding areas. At a 2:1 ratio (group size 6), the number of transfers between the high profitability and central areas increased, while the number between the low profitability and central areas did not alter significantly. At a ratio of 5:1 (group size 6), the number of transfers between the high profitability and central areas was unchanged, but the number between the low profitability and central areas decreased. Therefore, at profitability ratios of both 2:1 and 5:1 a similar trend occurred, namely a gradual shift in emphasis between the type of transfers; from those between the low profitability and central areas, to those between the high profitability and central areas.

At a group size of 12, and a profitability ratio of 1:1, the number of transfers per 100sec interval increased with elapsed time for both feeding areas (Table 5.3). This matches the result obtained at a group size of 6. No significant changes occurred at patch profitability ratios of either 2:1 or 5:1.

Considering the 900sec period as a whole, more transfers took place between the high profitability and central areas than between the low profitability and central areas at

Group size	Profitability ratio	Feeding area	b	P
6	1:1	LEFT	+0.385	***
		RIGHT	+0.363	***
	2:1	HIGH	+0.389	***
		LOW	+0.154	NS
	5:1	HIGH	-0.056	NS
		LOW	-0.356	**
12	1:1	LEFT	+0.298	**
		RIGHT	+0.412	***
	2:1	HIGH	+0.071	NS
		LOW	+0.063	NS
	5:1	HIGH	+0.118	NS
		LOW	-0.168	NS

Table 5.3 Results of regression analysis of the effects of elapsed time on the mean number of transfers per 100sec between each patch (high or low/left or right) and the central non-feeding area. *** $P < 0.001$, ** $P < 0.01$, NS= not significant.

Group size	Ratio	High	Low	T-value	P
6	1:1	3.59 (2.89)	3.46 (2.82)	0.52	NS
	2:1	3.73 (2.59)	2.49 (2.19)	5.37	***
	5:1	2.39 (2.16)	1.51 (1.83)	2.95	**
12	1:1	7.16 (3.19)	7.31 (3.81)	0.54	NS
	2:1	4.96 (3.37)	4.59 (3.34)	1.35	NS
	5:1	5.94 (3.27)	3.60 (2.44)	9.29	***

Table 5.4 Results of T-tests to compare the mean number of transfers per 100sec between each feeding area and the central non-feeding area, for the total 900sec trial duration. Results are given as mean and standard deviation (in parentheses). In the case of a 1:1 ratio High=left, Low=right. *** $P < 0.001$, ** $P < 0.01$, NS= not significant.

profitability ratios of 2:1 and 5:1 and a group size of 6 (Table 5.4). At a group size of 12, a significant difference occurred only at a profitability ratio of 5:1 (Table 5.4).

5.4 DISCUSSION

5.4.1 Stoneloach density and interference between individuals.

At group sizes of both 6 and 12 individuals and patch profitability ratios of 2:1 and 5:1, the number of fish found in the low profitability (poor) area was as predicted by the ideal free theory. However, the number found in the high profitability (good) area was significantly lower than expected. The remaining fish were found in the central area of the tank. No food was available in this area, so it was obviously not profitable for fish to remain there. As the observed number of fish in the good area fell further below the number predicted at a group size of 12 ($P < 0.001$, G-test) than at a group size of 6 ($P < 0.05$, G-test) an explanation which takes number of competitors into account seems a possibility.

Effects of interference in reducing foraging efficiency have been described in a number of bird species. Goss-Custard (1980) defined interference as a reversible, and more-or-less immediate, reduction in an individual's rate of food intake due to the effects of the presence of other competitors. Zwarts (1978) showed that the rate of

food intake of curlew *Numenius arquata* decreased as the density of birds rose. Redshank were similarly affected when feeding close together (Goss-Custard 1976).

Interference may reduce the feeding rate of individuals by several possible mechanisms (Goss-Custard 1980), for example by aggressive encounters over food (Goss-Custard 1977b, Silliman, Scott Mills & Alden 1977), disturbance from other birds whilst searching (Goss-Custard 1976), depression of prey availability (Goss-Custard 1970b) or by increasing use of poorer areas (Zwarts 1974, 1976).

Ens & Goss-Custard (1984) studied oystercatchers feeding on mussels *Mytilus edulis*. A group of 10 birds was studied in detail, and, of 8 birds for which adequate data was obtained, the intake rate of 6 decreased as oystercatcher density increased. A stable linear dominance hierarchy was observed in the birds studied, the birds affected all being subdominant individuals. Interference did not adversely affect the intake rates of the two most dominant individuals. The interference experienced by the subdominant birds took the form of intraspecific kleptoparasitism, and possibly, avoidance of dominant individuals by subdominants (Ens & Goss-Custard 1984).

During the many hours of observation needed to collect data from videotape, aggressive encounters between stone loach were never observed. This hopefully discounts aggressive encounters between competitors of the kind observed in birds by Goss-Custard (1977b) and Silliman, Scott Mills &

Alden (1977). Non-aggressive interference is, however, not ruled out.

From the results obtained at patch profitability ratios of 1:1 and 5:1, although not 2:1, the presence of stoneloach in the central part of the tank appears to be density-dependent. At a group size of 6, and ratios of 2:1 and 5:1, significantly fewer individuals than predicted were found in the good area, where 4 and 5 fish respectively were predicted by the ideal free distribution. At a ratio of 1:1 the ideal free prediction of 3 fish in each patch was met.

There are two possible explanations. The first is that any more than three fish could not fit comfortably into one of the feeding areas without leading to interference, causing some individuals to be forced into an inferior position in the central area. The second is that fish were unable to correctly assess patch profitability.

If the latter were the case, more fish than predicted would be expected in the poor area, where at least some gains should be possible. As this was not observed it is therefore assumed that interference occurred above a certain competitor density.

Further support for this hypothesis is provided by the results obtained at a group size of 12. At both unequal patch profitability ratios (2:1 and 5:1) fewer fish than predicted were found in the good area. Once again, the

number found in the poor area did not differ from the predicted values, of four and two respectively. At a profitability ratio of 1:1, however, significantly fewer individuals than predicted were found in one of the areas, and in the other the number was also fewer, though not significantly so.

This leads to the conclusion that at the larger group size interference occurred at a ratio of 1:1 as well as at ratios of 2:1 and 5:1, and therefore that 6 fish could not fit into a feeding area without interfering with each other.

As shown in Chapter 3, individual stoneloach differed in their ability to locate a concealed food source. It is unlikely that differences in foraging behaviour between individuals would be restricted simply to differences in their ability to find hidden food. It is therefore likely that individuals will differ in their susceptibility to the effects of interference.

Regrettably, it was not possible to determine whether particular individuals spent more time in the central area, which would be a possible means of determining whether some fish were more affected by interference than others, due to the relatively poor definition of the video picture. An additional problem found when the tanks were viewed from above, as in this experiment, was that fish occasionally went out of sight at the very edges of the tank, as they became obscured by the top frame of the tank. This was

unimportant when a measure of the *number* of fish in each area was required, as it was possible to remember how many fish were hidden in this way. However, it was not possible to reliably follow *particular* individuals.

As the number of fish found in the poor area at unequal patch profitability ratios was not greater than predicted, it is possible that a tactic of attempting to compete for space in the good area (and consequently being forced to reside on occasion in the central area) is more profitable than a tactic of accepting a permanent position in the poor area. Unfortunately, this hypothesis cannot be examined further, as this would necessitate a knowledge of individual gains.

5.4.2 Movements between areas: patch sampling

It is commonly assumed in the optimal foraging literature that animals forage in such a way as to maximise their fitness (eg Pyke, Pulliam & Charnov 1977, Krebs 1978, Cowie & Krebs 1979). Most authors agree that a convenient measure is the animal's rate of food intake whilst foraging, therefore animals will be expected to attempt to maximise their rate of food intake when foraging (eg MacArthur & Pianka 1966, Charnov 1973).

In an environment where predators do not have complete knowledge of habitat quality, they must sample the food patches in order to decide which is the best one to exploit. This could be achieved by first sampling the

available patches and then concentrating on the best, or by continuously moving from patch to patch, using recent experience to modify current and future decisions (Cowie & Krebs 1979). Krebs & Cowie (1976) found that flocks of great tits *Parus major* consistently sampled less profitable patches in the habitat. Caraco, Martindale & Whittam (1980) pointed out that it was adaptive for animals to continue to sample even a stable habitat, as this would enable them to respond to any changes which might occur.

Krebs, Kacelnik & Taylor (1978) investigated the behaviour of captive great tits in an environment containing two patches of different profitabilities. The birds had no prior knowledge of the environment, and could determine which patch was the best only by sampling. After an initial period of sampling, the birds settled down to exploiting the most profitable patch. In addition, Krebs, Kacelnik & Taylor (1978) found that the birds came to their decision most rapidly when the difference in relative patch profitability was greatest.

In the present study, the number of transfers across imaginary "borders" between each feeding area and the central area provides an indication of the amount of sampling by the fish. As in the previous chapter, this does not imply active sampling by the fish, although this may have occurred, however an increase in the number of transfers between areas of the tank will provide the fish with more opportunities to obtain information about the environment.

The total number of transfers decreased as the difference in profitability between the two patches increased. This result is compatible with that obtained by Krebs, Kacelnik & Taylor (1978), the explanation being simply that it is easiest to tell the two patches apart when the difference between them is greatest. However, the stone loach moved between the patches throughout the trial period, as evidenced by the continued occurrence of transfers. These could have been a result of both patch sampling and competition between individuals on the patches.

The sample-then-exploit tactic used in experiments by Krebs et al.'s great tits seems more likely when no conspecifics are present, and when patches do not become depleted during the course of the experiment. In contrast, in the present case a number of individuals were present, and patches were of a depleting nature. These differences are possible explanations for the different sampling tactic employed. The observations of Krebs & Cowie (1976) and Caraco, Martindale & Whittam (1980) mentioned above would seem to support this hypothesis.

As previously noted, more transfers took place between the good area and the central area than between the poor and central areas at patch profitability ratios of 2:1 (group size 6 only) and 5:1 (group sizes of 6 and 12). If the number of transfers had been equal, this would indicate that each transfer from good to poor areas (via the central area), or from good to centre and back to good, was matched

by one in the opposite direction or from poor to centre and back to poor. However, as significant differences were found in the cases stated, more transfers involving the good feeding area than the poor area must have taken place.

This provides further support for the earlier hypothesis that the effects of interference between foraging individuals was excluding fish from the high profitability area. It appears, therefore, that the fish became aware of the presence of high and low profitability patches, but of those which tried to feed on the former, not all were able to do so.

5.4.3 Do the results conform to an ideal free distribution, and if not, why not?

In all cases, the number of fish found in the poor area matched that predicted by the ideal free distribution. At unequal profitability ratios (2:1 and 5:1), and at both group sizes, the number of fish in the good area fell below the predicted number. This was probably due to interference between individuals which caused some fish to be excluded from the good area. It seems very likely that the assumption of the ideal free theory that all individuals have an equal competitive ability was violated, if the observations in Chapter 3 extend to aspects of the stone loach's feeding behaviour other than the ability to locate food.

It is interesting to note the length of time taken to

achieve a stable distribution. Such a distribution was observed after about 600sec (see Figure 15 (A-F)). This contrasts with times of below 60sec for the cichlid *Aequidens curviceps* (Godin & Keenleyside 1984) and about 240sec for sticklebacks (Milinski 1979). This difference is possibly caused by the olfactory nature of stoneloach foraging. Both sticklebacks (Milinski 1979) and flag cichlids (Godin & Keenleyside 1984) were feeding visually and also able to see each other. This would enable them to arrive at a stable distribution more rapidly than if olfactory and lateral line mechanisms had to be used by the fish firstly to find food and secondly to distribute themselves.

Parker (1984) distinguishes between two extreme examples of an ideal free distribution (see section 5.1.2). In a situation where patches become depleted, a Type 1 model is predicted (Parker 1984). However, the stoneloach distributions observed appear to be of a Type 2 nature (Parker 1984), albeit with a much slower response time. A possible explanation of this apparent paradox is that at the start of a trial the fish do not have complete knowledge of the habitat. Indeed, an approximately 1:1 distribution of fish between the two halves of the tank was noted at the beginning of the trial period at all patch profitability ratios (Figure 15 (A-F)).

As the fish were foraging non-visually, an individual which found the poor patch first and started to feed there could well take a long time to discover that another patch was

present. It was not possible for an individual to see others feeding elsewhere, and therefore be able to go there and sample the profitability of the alternative food supply. Instead, it would have to use information obtained olfactorily, which would take longer to obtain, or via the lateral line. Information obtained by these means would probably not provide the same degree of accuracy as a visual signal.

It is thus possible to explain the presence of a Type 2 rather than a Type 1 distribution, and also the length of time required to attain a stable distribution, by the non-visual means of foraging being employed by the fish in this experiment.

Postscript to Chapter 5

It is essential to distinguish between Type 1 and Type 2 ideal free models. Throughout Chapter 5, comparisons were made between the observed distribution and that predicted by a Type 2 model. However, as the patches became depleted during the course of the experiment, comparisons with predictions of a Type 1 model would have been more appropriate. This point should be kept in mind when reading the chapter.

CHAPTER 6

EXPERIMENT 4: GROUP SIZE AND THE MARGINAL VALUE THEOREM

6.1 INTRODUCTION

6.1.1 Aims of Experiment 4

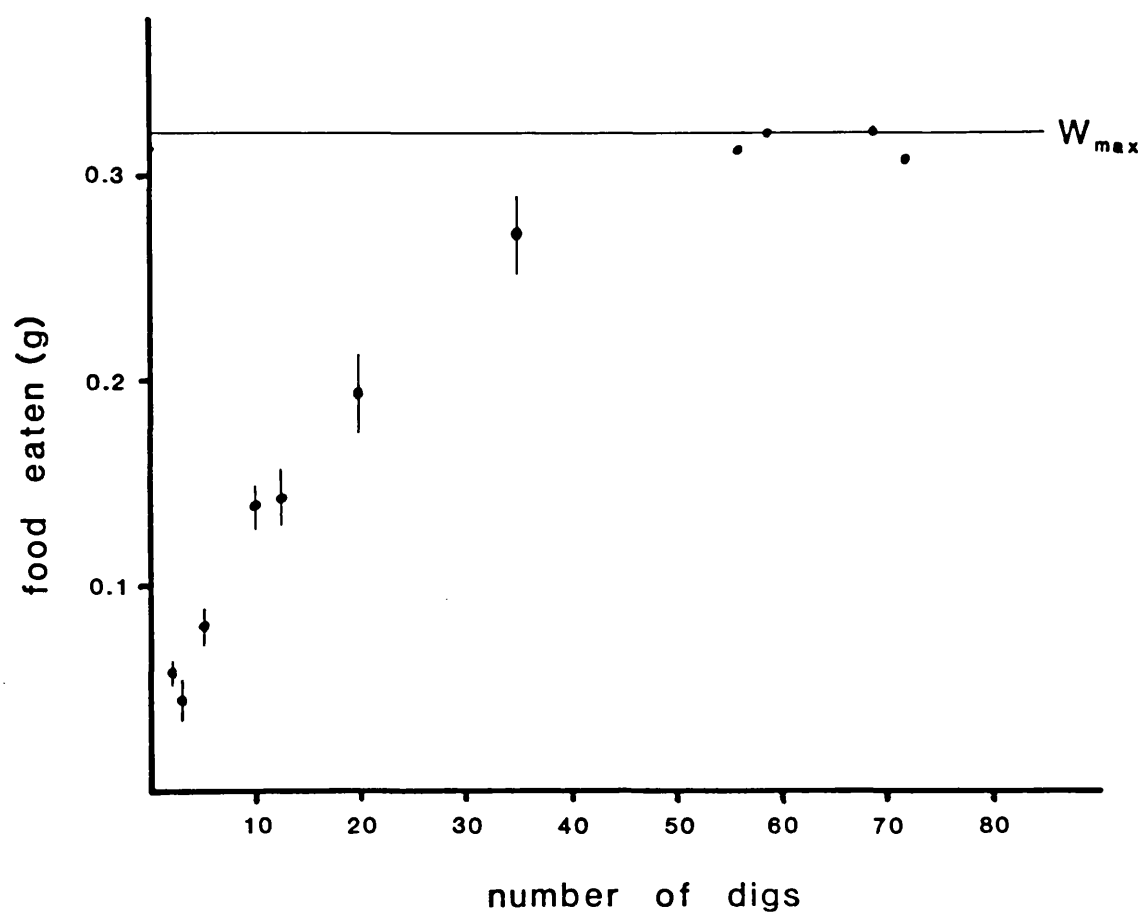
This experiment was originally conceived simply to provide evidence for the assumption made in preceding experiments that a greater quantity of food will be obtained by a stoneloach if it makes more digs. This accounts for the very small number of replicates obtained. However, given the observed relationship between the number of digs made, and the amount of food obtained (see Figure 19), it was considered worthwhile using the data to make quantitative predictions regarding residence time, with which some additional observations made in Experiment 1 could be compared.

Given the insubstantial nature of the data, firm conclusions will not be drawn, however it is felt that the results obtained may be a useful indicator for a future area of study.

6.1.2 Optimal allocation of time to patches

The ability to make predictions about an animal's foraging behaviour using mathematical models is a comparatively

Figure 19 The relationship between the number of digs made and the amount of food eaten. W_{max} indicates the initial amount of food contained in the patch, and consequently the maximum obtainable. Data are given as mean and (where appropriate) S.E.



recent development in the study of animal behaviour. Since Emlen (1966) and MacArthur & Pianka (1966), various authors have postulated a number of similar mathematical models, now collectively known as optimal foraging theory (OFT). A number of reviews of the subject have been published (eg. Pyke, Pulliam & Charnov 1977, Krebs 1978, Krebs, Houston & Charnov 1981, Krebs, Stephens & Sutherland 1983, McNair 1983, Hart in press). The models all assume that animals forage in such a way as to maximise their fitness, where the efficiency of a foraging animal is measured in terms of a "currency", usually energy (Schoener 1971).

Pyke, Pulliam & Charnov (1977) identified several areas within OFT. Of concern here is the optimal allocation of time to patches. The earliest study was probably that by Gibb (1958, 1960), who suggested the theory of "hunting by expectation", whereby animals come to expect a certain quantity of food from a patch, and remain in the patch until they have obtained that amount.

Krebs, Ryan & Charnov (1974) studied patch use in chickadees, *Parus atricapillus*, and found that their results were consistent with an optimal foraging model of patch use (Charnov 1973, 1976) rather than with Gibb's model of hunting by expectation. Charnov's (1976) "Marginal Value Theorem" (MVT) has since been studied by various authors (see Krebs, Stephens & Sutherland 1983).

If a predator is feeding on patchily distributed prey, it must decide when to leave one patch and move on to another,

in order to maximise its' rate of energy intake. As the animal feeds on a patch, the availability of food to the animal becomes depressed (Charnov, Orians & Hyatt 1976), and its' intake rate falls. The relationship between time in the patch and cumulative net food gain follows a curve, which rises rapidly at first and then levels out into an asymptote. A time will come when the animal's rate of food intake drops to a point at which it would do better to leave the patch and move elsewhere. This point may be predicted by means of the MVT (Charnov 1976).

The optimal solution is that the animal should choose its' residence time (RT) (time in the patch) so that it leaves when its' marginal capture rate (the rate of food capture immediately before leaving) drops to the average capture rate for all the food patches in the habitat. The MVT makes the assumption that the environment contains patches of different quality, each having its' own curve of cumulative net food gain with increasing residence time (Charnov 1976).

A further prediction of the MVT is that a longer travel time (the time required to get to the patch) will result in a longer residence time.

Krebs, Ryan & Charnov (1974) postulated that the marginal capture rate could be estimated from the "giving up time" (GUT), which is the time between the last capture and the time of leaving the patch, and that the expected marginal capture rate is inversely proportional to the giving up

time. The optimal foraging predictions that the same GUT should be observed for all patch types within a habitat, and that in better habitats where the capture rate is higher the GUT should be shorter, were met in experimental tests (Krebs, Ryan & Charnov 1974).

McNair (1982) has suggested that the MVT is specifically a residence time theory, and as such should not be used to make predictions about GUTs. McNair (1982) went on to propose an alternative model, based on giving up time, which predicts that GUT will be positively correlated with patch quality within habitats. He also stated that the MVT was a specific case of his own (McNair 1982) more generalised model.

Despite their differences however, both the marginal value theorem and McNair's alternative model based on GUTs predict that foragers should spend more time, and obtain higher gains, in better patches.

6.2 METHODS

The general methods used in this experiment were as described in Chapter 2. Four replicate groups of fish were used, each comprising two individuals. A group size of two, rather than one, was used as there was less likelihood of the fish not finding the food (see Table 3.6).

A single, centrally-placed, patch (see section 2.5, and Figure 1) containing 0.4g of tubificid worms was introduced

into the tank, and the fish allowed to make a preset number of digs into it, in order to obtain food. The different numbers of digs examined are shown in Table 6.1. On some occasions the fish were allowed to feed until all of the worms were apparently removed.

When the combined number of digs made by both fish in the group reached the required value, the patch was carefully removed. It was possible to combine the number of digs made by both fish in this way, as the objective was simply to determine how much food was removed from the patch by a certain number of digs made by the two fish.

Once the patch had been removed a second was added, containing 1.0g of food. This amount was in excess of that which the two fish could consume in the time available. This ensured that the fish's hunger level and consequent feeding tendency (see McFarland & Houston 1981) remained constant throughout the course of the experiment, regardless of the amount of food obtained from the first patch.

The remaining worms were removed from the test patches by tipping then into a small bucket of water. By swirling the gravel around, any worms floated clear and were poured off into a filter funnel, where they collected on filter paper. The worms were then allowed to drain for 30min, and were then removed using a pair of fine forceps, and weighed. Subtraction of the remaining weight from the starting weight (see below) gave a value for the amount of worms

consumed. The effect of the standardised draining procedure was taken into account by subjecting unexploited patches (containing 0.4g) to the procedure and then reweighing. A value of 0.319g was obtained, and this value was therefore taken to be the starting weight: ie the maximum weight of tubificids available.

6.3 RESULTS

6.3.1 The relationship between residence time and food intake

The amounts of food removed from the patch for different numbers of digs made by the fish are given in Table 6.1, and are shown graphically in Figure 19.

It was not possible to directly determine the relationship between residence time (time spent on the patch) and food intake, as a group size of two fish was chosen in order to increase the likelihood of the patch being found (see Experiment 1, Table 3.6). Therefore, even if the number of digs made by each fish was known, and its' residence time, it would not be possible to determine exactly how much food each fish had consumed simply by dividing the total amount of food eaten by the proportion of the total number of digs which were made by each fish.

It was, however, possible to determine very accurately the total amount of food consumed in a particular number of digs. Using this information, the relationship between

food intake and residence time was determined indirectly.

6.3.2 Applying the Marginal Value Theorem

Using additional data obtained whilst performing Experiment 1 (Chapter 3), on the duration of the subject fish's first visit to the patch (see Table 6.1), and correlating this with the number of digs made during the visit, a regression line showing the relationship between the two variables was obtained (Figure 20). Using the plotted regression line, the different numbers of digs examined in this experiment were converted into their associated residence times.

From the equation

$$\ln \frac{W_{\max} - W}{W_{\max}} = -\lambda RT \quad (1)$$

where W_{\max} = the maximum amount of food available, W = the observed food intake, RT = residence time, and λ = a rate constant, a regression line was plotted ($R^2 = 0.70$, $F = 121.0$, $P < 0.001$) between food intake (W) and residence time (RT), the slope (b) of which is equivalent to the rate of change of food intake (λ) over time (Figure 21).

The value of λ (-0.00322) from equation (1) above was then substituted into the equation

$$W = W_{\max}(1 - e^{-\lambda t}) \quad (2)$$

By substituting values of t at 10sec intervals a curve of

Number of digs	Number of replicates	Worms eaten (g)	S.D.	Residence time (s)*
2	6	0.0582	0.0186	30.5
3	6	0.0463	0.0217	47.0
5	9	0.0830	0.0147	79.0
10	9	0.1388	0.0309	158.0
15	8	0.1426	0.0438	239.0
20	8	0.1949	0.0539	320.0
35	4	0.2724	0.0350	560.0
56	1	0.3142	_____	895.0
59	1	0.3190	_____	947.0
69	1	0.3190	_____	1109.0
72	1	0.3086	_____	1154.0

Table 6.1 The relationship between the number of digs made and the amount of worms eaten. This data was used in Figure 19.

* Residence time obtained from number of digs, using Figure 20 (data was obtained from Experiment 1).

Figure 20 The relationship between the number of digs made during a visit, and visit duration. Data was obtained from Experiment 1. The regression line and 95% confidence limits are plotted.

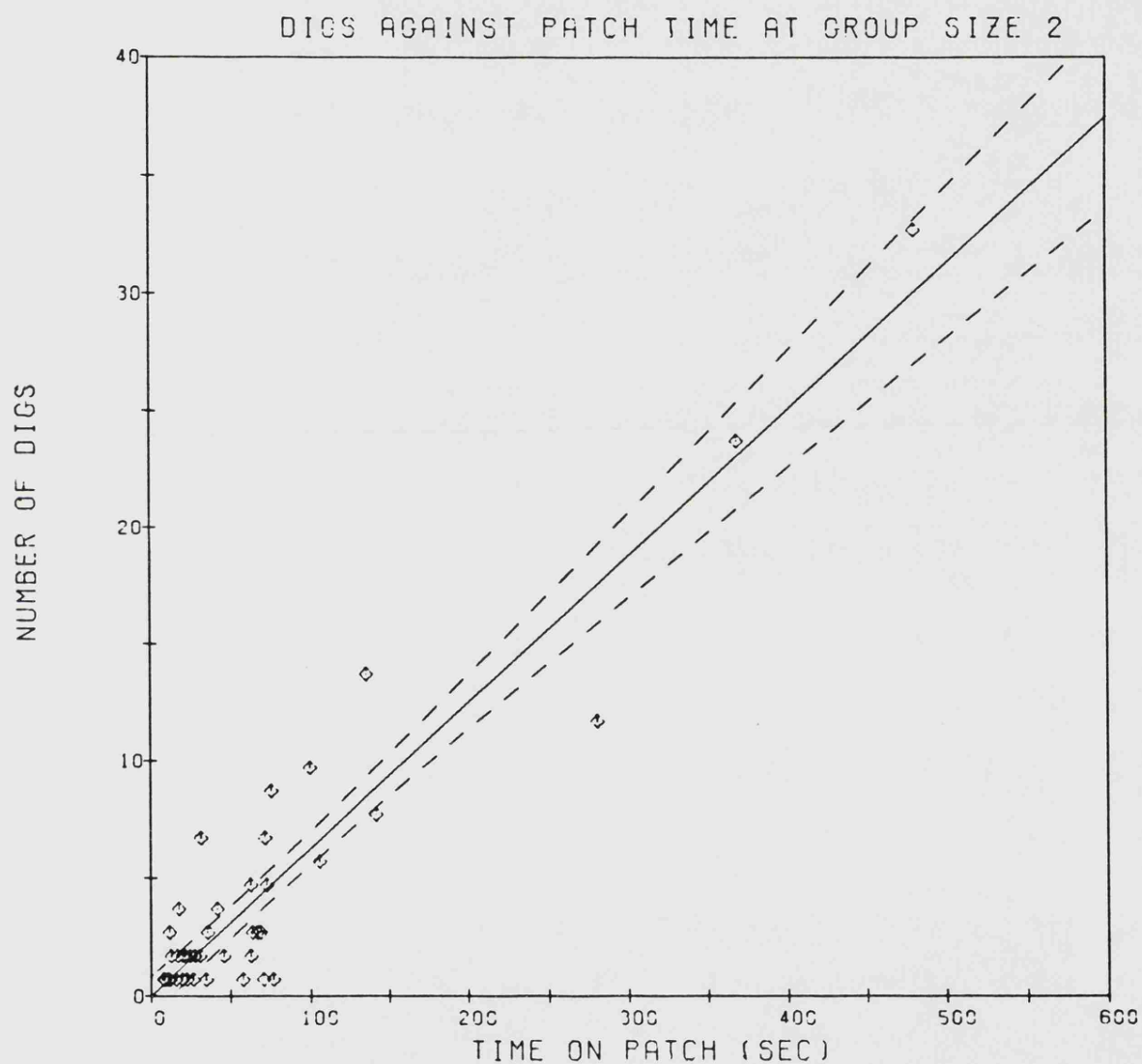
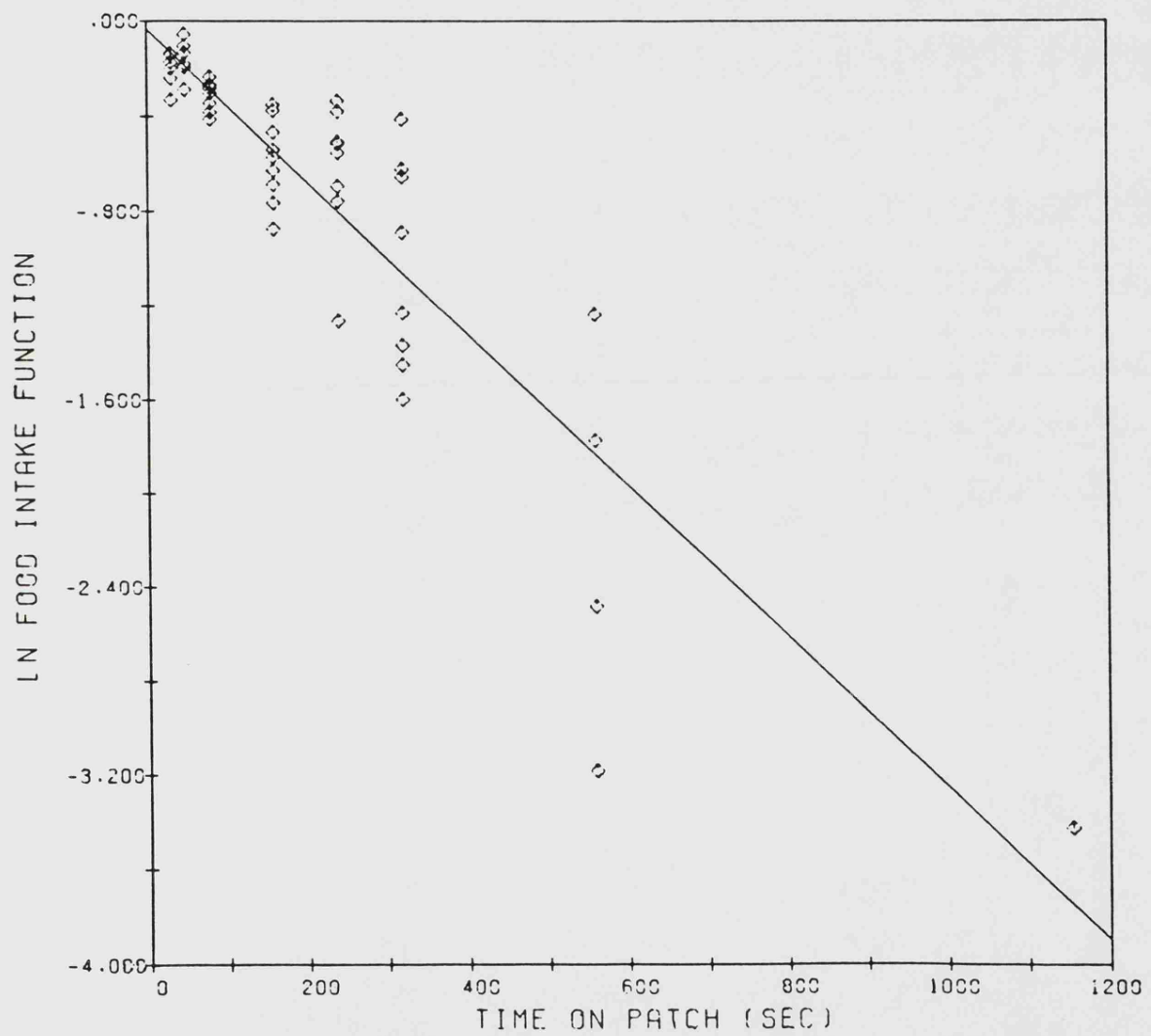


Figure 21 The relationship between food intake rate and residence time, obtained using Equation (1). The slope of the plotted regression line (λ) was then substituted into Equation (2).



the relationship between cumulative food intake and residence time was produced (Figure 22).

By drawing a tangent originating from the travel time obtained in Experiment 1 (for each group size of one, two and five individuals), and dropping a perpendicular from the point at which the tangent grazed the curve, to the X-axis, the predicted residence time was obtained (Krebs 1978, Krebs & McLeery 1984). The predicted residence time was then compared with the actual residence time obtained in Experiment 1. The predicted and observed residence times are given in Table 6.2.

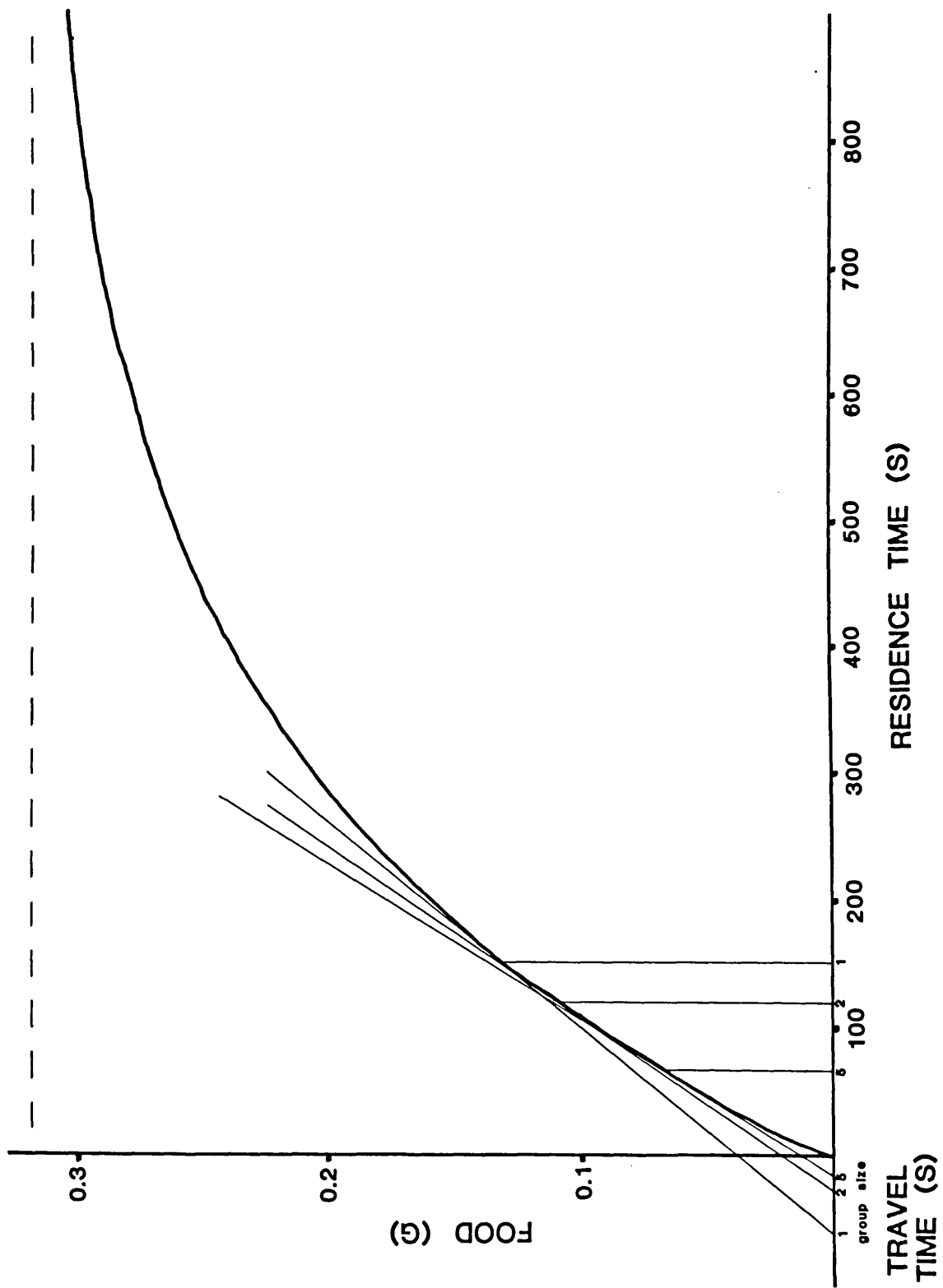
At a group size of one, the marginal value theorem gave a good prediction of residence time. However, when conspecifics were present the predicted residence time was approximately 1.7 (group size of two) and 2.0 (group size of five) times longer than the observed residence time.

6.3.3 Giving up time

The effect of patch quality on giving up time (GUT) was examined using data obtained in Experiment 2, by analysing the relationship between GUT, ie the time between "capturing" the last food item and leaving the patch, and patch quality, defined as an arbitrary initial value devalued according to the number of digs already made on the patch. Each time an individual returns to a depleting patch, the patch quality encountered will be lower than that encountered during the previous visit, so that, in

Figure 22. (On following page).

Plot of cumulative food intake against residence time, obtained using Equation (2). Data for travel times were obtained from Experiment 1, and used as shown to determine predicted patch residence times. The dotted horizontal line indicates the maximum amount of food obtainable, W_{max} . See text for explanation.



group size	travel time (s)	observed R.T. (s)	predicted R.T. (s)
1	61.0	146.9	152.0
2	27.0	69.1	120.0
5	14.5	32.8	67.0

Table 6.2 Observed (from Experiment 1) and predicted (from Figure 22) residence times for each group size.

effect, the patch is a different one to that visited previously.

No change in GUT was found with a decrease in patch quality at either a group size of two (regression analysis: $b=0.07$, $n=272$, $R=0.05$, $F=0.79$, $P=0.38$) or five individuals ($b=0.08$, $n=381$, $R=0.06$, $F=1.26$, $P=0.26$). This result is consistent with the optimal foraging prediction that GUTs should be constant for all patches within a habitat (eg Hart in press). However, the mean GUT was longer at a group size of two than at a group size of five (mean for groups of 2 = 13.28sec, mean for groups of 5 = 6.36sec, $P<0.001$, t-test). The reduction in GUT is consistent with the reduction in visit duration with an increase in group size (Experiment 2).

6.4 DISCUSSION

Using the marginal value theorem (Charnov 1976), it is possible to make predictions as to how long an optimal predator should remain in a food patch, where patch quality, habitat quality, and travel time between patches may be variable. In this study, the effects of group size, a previously unconsidered variable, are examined.

Various studies have yielded results which were consistent with the predictions of models of optimal patch use (eg Smith & Sweatman 1974, Zach & Falls 1976, Cowie 1977, O'Connor & Brown 1977, Pyke 1978, Sih 1980, Munger 1984). As Munger (1984) points out, with the exception of that by

Cowie (1977), these studies all tested qualitative predictions, so although the observed behaviours were found to be more efficient than random behaviour, they were not necessarily optimal.

In the present study, a good match between predicted and observed residence times occurred at a group size of one, but at group sizes of two and five individuals the observed residence time fell well short of that predicted. There are several possible explanations for this. Firstly, increased interference experienced by the subject fish on the patch may have "encouraged" it to leave the patch sooner than the optimal time. This would appear to be a strong possibility, but probably only at a group size of five individuals (see Chapter 5).

A second possibility is that a faster digging rate at the larger group size (see Figures 9 and 10, mean for groups of 2 = 0.104 digs per sec, mean for groups of 5 = 0.182 digs per sec, $P < 0.001$, t-test) would enable a fish to obtain more food in a given time. This would have the effect of giving the fish a higher rate of food intake, which would cause the patch to become depleted more rapidly, which in turn would cause the fish to reach the marginal rate sooner. If this occurred, a different food intake/residence time curve would be required for each digging rate, and therefore group size. It is therefore possible that the fish were leaving at the optimal time for each set of circumstances, but that the time predicted by the theory was wrong.

There is also the added complication of digging rate decreasing as the patches become depleted (see Figures 9 to 14). A change of this nature would increase the time taken for the fishes' rate of food intake to decrease to the marginal rate, thereby increasing residence time. Digging rate decreased more rapidly at a group size of five than at a group size of two (Figures 11 to 14), which may help to offset possible effects of the higher digging rate observed at the larger group size.

The MVT as originally proposed (Charnov 1973, 1976) was designed to predict the optimal residence time for a solitary predator, and in this study a good match between the observed and predicted residence times was obtained at a group size of one. At larger group sizes however, the presence of conspecifics will introduce effects which the model was not formulated to account for, so it is perhaps not surprising that differences between the observed and predicted residence times were found.

It was not possible in this study to determine whether or not the results were consistent with predictions of alternative models, such as hunting by expectation (Gibb 1958, 1960), or the use of a giving up time strategy (McNair 1982). These alternatives should however not be ruled out as possible decision rules with which stoneloach may decide how long to remain in a patch.

Postscript to Chapter 6

The application of the Marginal Value Theorem to the results obtained in Chapter 6 is not, in retrospect, considered to be justified. There are two reasons for this decision. Firstly, only a single patch was present, so that an individual was unable to leave one patch and go to another. Secondly, the Marginal Value Theorem is designed to make predictions regarding the optimal patch residence time of a solitary predator, whereas in this experiment more than one individual was present.

This does not however invalidate the experiment; the original aims of which, expressed in section 6.1.1, remain valid.

CHAPTER 7

GENERAL DISCUSSION

7.1 The pros and cons of group membership

There are several advantages to be gained by an individual from group membership. As group size increases, an individual's protection from predators may improve, as it may be possible to detect predators earlier (Pulliam 1973, Kenward 1978, Magurran, Oulton & Pitcher 1985). Seghers (1981) has shown that when a fish is a member of a group it needs to spend a smaller proportion of its time being vigilant, and as a consequence has more time available for other activities (Bertram 1978), such as foraging.

Birds in groups spend a high proportion of their time looking up, or "scanning". This behaviour increases the likelihood of noticing an approaching predator, but also has the effect of decreasing the scanners' feeding rate. Using a game theoretical approach, Pulliam, Pyke & Caraco (1982) predicted optimal scanning rates for Juncos following either a selfish or a co-operative scanning strategy. They found that experimental data was closer to the predicted co-operative rate than to the predicted selfish rate. A judge strategy, whereby an individual should stop scanning if it noticed another flock member not scanning was found to be evolutionarily stable. Therefore, so long as no group members "cheat" the scanning system,

individuals will benefit from the extra safety provided by the greater likelihood of early predator detection found in a group.

The more rapid location of a food supply seen in birds (Krebs, MacRoberts & Cullen 1972) and fish (Pitcher, Magurran & Winfield 1982, Street & Hart in press) is a further advantage of group membership, as is the improved ability of a larger group to recover feeding performance after an alteration in the positions of different profitability patches (Pitcher & Magurran 1983).

However, there are also disadvantages to an increase in group size, in the form of increasing competition within the group for the available resources (Bertram 1978). An example of this was shown by Street, Magurran & Pitcher (1984) who found that the handling time of each food item by goldfish decreased with an increase in group size. This was presumably due to increased competition perceived by group members. Street et al (1984) point out that such "bolting" of food is likely to bear digestive costs.

The existence of both costs and benefits to group membership suggest the possibility of an optimal group size, where the average individual does best (Bertram 1978). At this group size the effects of competition within the group would not be too great, and the members would derive reasonably good protection from predators, and also benefit from the social advantages of group membership (see Pitcher, Magurran & Allan 1983).

However, using hypothetical game theory models Clark & Mangel (1984) and Pulliam & Caraco (1984) have independently demonstrated that such an optimal group size would not be stable. There would be a constant tendency to "overflock" (Clark & Mangel 1984), which in fact is an evolutionarily stable strategy. Pitcher (in press) makes the analogy with the "tragedy of the commons" (Hardin 1968), whereby more and more predators (originally fishing boats) join in the exploitation of a limited resource and everybody's share becomes smaller. In this way, the members of very large shoals may obtain zero feeding benefit, but may remain together for protection from predators (Pitcher in press).

Clark & Mangel (1984) suggest that overflocking will to some extent offset the advantages of increased feeding rates in larger groups, which result from the sharing of information among group members. They also note that individuals in larger groups may possess less variable feeding rates, and that the tendency to group will be stronger, in more variable environments. Both Pulliam & Caraco (1984) and Sibly (1983) observe that the model predicting the stability of a greater than optimal group size will strictly apply only when individuals all have an equal competitive ability, and each feeds where it can maximise individual gain. In effect this is a modification of Fretwell's (1972) Allee-type ideal free model (Sibly 1983).

In this study individuals benefitted from a reduction in the time taken to locate a food supply which occurred with an increase in group size. It is also possible that the higher level of searching activity evident at a larger group size would give added "protection" against fluctuations in food supply. In both Experiments 2 and 3 it seems likely that interference occurred between competitors which would result in a reduction in overall food intake and therefore limit the benefits to be obtained from an increase in group size.

As individuals differed in their foraging ability, as demonstrated by the variation in their ability to locate food, the models proposed by Sibly (1983) and Pulliam & Caraco (1984) may not apply. It is certainly possible that the increase in costs with increasing group size could serve to limit the tendency to overflock. Information regarding the effects of group size on predator detection would be useful here, as another factor which may be involved in the balance between costs and benefits.

7.2 Group size and patch use

Stoneloach were able to locate a hidden food source more rapidly when group size increased from one to five individuals (Experiment 1). However, consistent differences in individual food-finding ability suggest that that a poor finder had more to gain from group membership than a good finder. Despite these differences, however,

all fish exhibited a shorter patch location time when group size increased.

When the exploitation of patches over a longer period was considered, it was found that fish in a group of five individuals made fewer digs on the patches than did fish in a group of only two. This suggests that the fish in the larger group may in fact have obtained less food. Pitcher & Magurran (1983) suggested that goldfish in a group of five could afford to be "less optimal" when foraging than those in a group of two because their total foraging time was greater. It is possible that, as Pitcher & Magurran (1983) postulated, fish in a smaller group perceived themselves to be at a greater risk from predators, even though an overt threat may have been absent. Minnows in a larger group were found to be less timid (Magurran & Pitcher 1983), and were able to detect an approaching model predator more rapidly (Magurran, Oulton & Pitcher 1985) than fish in a smaller group.

7.3 Information and patch use

An important effect of increased group size was an increased opportunity for sampling of the patches. This was observed in Experiment 2, both when the patches were equal, and when they were different in their profitability, and also in Experiment 3.

The significance of sampling has been studied both experimentally and theoretically. In an experimental

study, Krebs, Kacelnik & Taylor (1978) examined the way in which predators sampled the environment, using a simplified version of the "two armed bandit" model. Their model was used to predict the amount of sampling of two sites necessary before a predator could settle down to exploitation of the best patch. The resulting balance between sampling and exploitation was found to be close to the optimal solution which would maximise the amount of food obtained during the foraging period. As previously noted, Caraco, Martindale & Whittam (1980) suggested that continued sampling can provide an insurance against future changes in the environment.

Under the conditions imposed by the marginal value theorem (Charnov 1976), a forager does not gain any information whilst foraging, and should leave the patch when its instantaneous rate of food intake drops to the environmental average. Oaten (1977) recognised this, and made a theoretical analysis of foraging on patchily distributed prey in a stochastic environment. The complexity of Oaten's (1977) paper has been an obstacle to its applicability, and it has done little to alter the general approach to patch use problems (McNamara & Houston 1985).

Several simplifications of the model have followed (eg Green 1980, 1984). McNamara (1982) made more general predictions for sampling in a stochastic environment, the main conclusion being that if a predator is gaining information about a food patch whilst foraging there, it

should stay longer than the length of time predicted by the marginal value theorem. A small reduction in the rate of food intake from the maximum possible may be worthwhile if the predator is able to gain some extra information about the environment (Krebs & McLeery 1984).

In Experiment 2, fish in a group of five individuals may have experienced a lower food intake than those in a group of only two. However, the overall greater level of searching activity in the larger groups would have given individuals more opportunities to obtain information about their environment, which may have been of greater benefit than the short-term maximisation of intake rate (Krebs & McLeery 1984).

McNamara & Houston (1985) made further simplifications in order to give the model more general applicability, and made predictions for an environment where patches could contain only a single food item. Two types of environment were discussed, firstly where some patches were empty, and secondly where all patches contained a food item but the ease of obtaining the item varied from patch to patch. In both situations, as an animal spent time in a patch without obtaining a reward it gained information about the patch; ie whether or not the patch contained a food item, and, if it did, how difficult the item was to obtain. The information that could be obtained could make it optimal for the animal to leave a patch without having obtained any food. Additionally, information was easier to obtain when

the variability between patch types increased (McNamara & Houston 1985).

Support for the latter prediction was obtained in Experiment 3 (Table 5.2), where the total number of movements between areas of the tank decreased as the difference in profitability between the patches increased. This indicates that the fish became better able to distinguish between the two patches as the difference between them increased.

The model proposed by McNamara & Houston (1985), in common with earlier stochastic models (Oaten 1977, Green 1980, McNamara 1982) and the marginal value theorem itself (Charnov 1976), makes predictions regarding the behaviour of a solitary predator. As the difference in profitability between patches increases, information becomes easier to acquire (McNamara & Houston 1985), and less sampling is required to distinguish between them (Krebs, Kacelnik & Taylor 1978).

An increase in group size can have a similar effect. For example, in a study by Pitcher & Magurran (1983) a greater amount of sampling occurred at a larger group size, which enabled members of larger groups to recover feeding performance more rapidly after a switch in patch profitability. This was achieved despite the fact that 80% of the group members were unaware of the new arrangement.

In Experiment 2 the stoneloach became more "quality

conscious" when group size increased from two to five individuals. There was a greater increase in the number of visits made to the good patch than there was to the poor patch when group size increased. Additionally, search time was increased at the expense of time spent feeding on the poor patch. This is a good example of a situation where it may be worth sacrificing some food intake for a greater knowledge of the environment.

7.4 Stoneloach distribution- "an ideal free" distribution?

In Experiment 3, the distribution of individuals between the two feeding areas of the tank did not, in most cases, conform to an ideal free distribution (Fretwell & Lucas 1970) as the number of fish found in the higher profitability area was lower than predicted. A possible explanation is the occurrence of interference between individuals, causing some to "accept" an inferior position in the tank.

No aggression was noticed between individuals, and the exact mechanism by which the observed distribution was arrived at remains unknown. However, it is suggested that individuals differed in their susceptibility to interference, in much the same way as they were found to differ in their foraging ability in Experiments 1 and 2. It seems likely that individuals which were poor at finding food also had a poor foraging performance generally, and may therefore have been more adversely affected by interference from conspecifics.

An important assumption of the ideal free distribution (Fretwell & Lucas 1970), that all individuals have an equal competitive ability, is thus perhaps not valid in this study. Territoriality or resource defence did not occur, so a discussion of the observed distribution in terms of an ideal despotic distribution (Fretwell & Lucas 1970) is unjustified.

In his study with sticklebacks, Milinski (1979) found that a group of six fish distributed themselves in accordance with the predictions of an ideal free distribution at patch profitability ratios of 2:1 and 5:1. In a subsequent study, Milinski (1984) was able to monitor individual food gains, which was not possible in his earlier experiment. Although fish differed in their competitive ability, a distribution compatible with the ideal free prediction was obtained. The good competitors in the group distributed themselves more rapidly than the poor competitors, the latter individuals taking the distribution of the good competitors into account, in addition to differences in patch profitability.

In Milinski's study an apparently ideal free distribution was found in spite of the fact that one of the model's most fundamental assumptions was violated (Milinski 1984).

Milinski (1984) quotes an unpublished study similar to that published, except for the fact that the water fleas used to produce drift food patches were made very conspicuous. In

this case only the three good competitors achieved a stable distribution, in the ratio of patch profitabilities. The three poor competitors did not achieve a stable distribution, but continually switched between the patches, and therefore had a lower food intake. However, their switching was part of an exploitation strategy. By returning to a central position in the tank and then rushing to the patches, the fish could grab items missed by the resident good competitors. This strategy was however not possible when the food items were less conspicuous. Milinski (1984) suggests that the poor competitors were following a strategy designed to make the best of the situation.

Milinski's (1984) suggestion that the poor competitors were having to make the best of a bad job is similar to that made in this study; that poor competitors may do better by settling for a place in the centre of the tank away from the good competitors and making occasional incursions into the feeding areas, particularly the more profitable. As far as can be judged, the fish in the central part of the tank were not always the same individuals. A knowledge of the location and gains of each individual may make it possible to determine whether such a strategy was being employed.

7.5 Suggestions for further study

Throughout this study a number of replicate fish were used, but in Experiment 1 in particular, and also Experiment 2,

significant differences between them were observed. For example, some individuals benefitted more than others from an increase in group size. It is obviously very important to consider the consequences of differences in foraging ability between individuals.

The results of Experiment 3 suggest that interference occurred between competing individuals, which seems likely to have caused fish to have a lower food intake, as they spent a proportion of their time in the centre of the tanks, away from food supplies, rather than on the patches. This experiment could be made considerably more conclusive if it were possible to follow each fish throughout the trial period. This would provide information on the proportion of time spent by each fish in the centre of the tank, and would also make it possible to ascertain whether individual stoneloach differ in their susceptibility to interference (see Sutherland & Parker 1985).

It was not originally intended, in Experiment 4, to make quantitative predictions for residence time, nor indeed to consider the Marginal Value Theorem (Charnov 1976). The experiment was conceived simply as a control experiment, so some excuse can be made for the rather insubstantial nature of the data. However, the failure of the marginal value theorem to correctly predict residence time at group sizes other than that of a single individual suggests a potentially important area for further study.

Finally, it would be interesting to study stoneloach

foraging in nature, or at least in larger, more natural conditions in the laboratory. The environment was, of necessity, much simplified, and the experiments were beset with difficulties arising from the need to employ infra-red lighting and video equipment, which greatly limited the possible definition of video recordings.

Very little is known of the behaviour of the stoneloach in its' natural habitat. It is very likely that the crepuscular nature of its' activity pattern will present a major obstacle to an increase in the knowledge of the species' behaviour in more natural surroundings.

7.6 Summary of the effects of group size on stoneloach foraging behaviour

An increase in group size has both inherent costs and benefits to a foraging stoneloach. Among the costs are an increase in competition, and a possibility of interference between competitors, to which some individuals may be more susceptible than others.

Benefits include the more rapid location of a food supply, although here some may benefit more than others, a greater sensitivity to patch profitability, a greater emphasis on sampling of the environment, and a possibility of a greater level of overall vigilance.

The ways in which group size affects the foraging of stoneloach are inevitably determined to some degree by the

non-visual nature of the fish's foraging. An example of this is the much longer time span over which changes occurred, when comparisons are made with studies of visually foraging species. However, it seems that the foraging behaviour of a social group of stoneloach can be affected by alterations in group size in much the same way as that of a visually foraging fish species.

LITERATURE CITED

- Barnard, C. J. 1980. Flock feeding and time budgets in the house sparrow, *Passer domesticus*, L.. *Animal Behaviour*, 28, 295-309.
- Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers: a general model and its applications to captive flocks of house sparrows. *Animal Behaviour*, 29, 543-550.
- Bateson, W. 1890. The sense organs and perceptions of fishes; with remarks on the supply of bait. *Journal of the Marine Biological Association UK.*, 1, 225-256.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology: An Evolutionary Approach*. Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.
- Bertram, B. C. R. 1980. Vigilance and group size in ostriches. *Animal Behaviour*, 28, 278-286.
- Bleckmann, H. In Press. The role of the lateral line in fish behaviour. In: *The Behaviour of Teleost Fishes*. Ed. by T. J. Pitcher. Beckenham: Croom Helm.
- Bryant, D. M. 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuarine and Coastal Marine Science*, 9, 369-384.
- Burdeyron, H. & Buisson, B. 1982. On a circadian endogenous locomotor rhythm of loaches (*Noemacheilus barbatulus* L., Pisces, Cobitidae). *Zoologische Jahrbuecher. Abteilung fuer Allgemeine Zoologie und Physiologie der Tiere*, 86, 82-89.
- Caraco, T. 1979. Time budgeting and group size: a test of theory. *Ecology*, 60, 618-627.
- Caraco, T. 1980. Stochastic dynamics of avian foraging flocks. *American Naturalist*, 115, 262-275.
- Caraco, T. 1983. White-crowned sparrows (*Zonotrichia leucophrys*): foraging preferences in a risky environment. *Behavioral Ecology and Sociobiology*, 12, 63-69.
- Caraco, T. & Chasin, M. 1984. Foraging preferences: response to reward skew. *Animal Behaviour*, 32, 76-85.
- Caraco, T., Martindale, S. & Whittam, T. S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, 28, 820-830.
- Caraco, T., Martindale, S. & Pulliam, H. R. 1980. Avian time budgets and distance to cover. *Auk*, 97, 872-875.

- Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Unpublished Ph.D. thesis, University of Washington.
- Charnov, E. L. 1976. Optimal foraging; the marginal value theorem. *Theoretical Population Biology*, 9, 129-136.
- Charnov, E. L., Orians, G. H. & Hyatt, K. 1976. Ecological implications of resource depression. *American Naturalist*, 110, 247-259.
- Clark, C. W. & Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. *American Naturalist*, 123, 626-641.
- Clark, F. & Ison, S. J. In Preparation. Colonisation of Rutland Water by *Oligochaetes*.
- Cowie, R. J. 1977. Optimal foraging in great tits (*Parus major*). *Nature*, 268, 137-139.
- Cowie, R. J. & Krebs, J. R. 1979. Optimal foraging in patchy environments. In: *Population Dynamics*. Ed. by R. M. Anderson, R. D. Turner & L. R. Taylor. Oxford: Blackwell.
- Davies, N. B. & Halliday, T. R. 1979. Competitive mate searching in common toads, *Bufo bufo*. *Animal Behaviour*, 27, 1253-1267.
- Dijkgraaf, S. 1962. The functioning and significance of the lateral line organs. *Biological Reviews*, 38, 51-105.
- Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist*, 100, 611-617.
- Ens, B. J. & Goss-Custard, J. D. 1984. Interference between oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *Journal of Animal Ecology*, 53, 217-231.
- Filek, V. W. 1960. Vergleichende verhaltensstudien an grundfischen. *Zeitschrift fur Tierpsychologie*, 17, 420-426.
- Fraser, D. F. & Sise, T. E. 1980. Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. *Ecology*, 61, 790-797.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton: Princeton University Press.
- Fretwell, S. D. & Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, 19, 16-36.

- Gibb, J. A. 1958. Predation by tits and squirrels on the eucosmid *Ernarmonia conicolana* (Heyl.). *Journal of Animal Ecology*, 27, 275-296.
- Gibb, J. A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis*, 102, 163-208.
- Godin, J-G. J. & Keenleyside, M. H. A. 1984. Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory. *Animal Behaviour*, 32, 120-131.
- Goss-Custard, J. D. 1970a. The responses of redshanks (*Tringa totanus* (L.)) to spatial variation in the density of their prey. *Journal of Animal Ecology*, 39, 91-113.
- Goss-Custard, J. D. 1970b. Feeding dispersal in some overwintering wading birds. In: *Social Behaviour in Birds and Mammals*. Ed. by J. H. Crook. London: Academic Press.
- Goss-Custard, J. D. 1976. Variation in the dispersion of redshank *Tringa totanus* on their winter feeding grounds. *Ibis*, 118, 257-263.
- Goss-Custard, J. D. 1977a. Predator responses and prey mortality in redshank *Tringa totanus* (L.) and a preferred prey, *Corophium volutator* (Pallas). *Journal of Animal Ecology*, 46, 21-35.
- Goss-Custard, J. D. 1977b. The ecology of the Wash. III. Density related behaviour and the possible effects of loss of feeding groups on wading birds (Charadrii). *Journal of Applied Ecology*, 14, 721-739.
- Goss-Custard, J. D. 1980. Competition for food and interference among waders. *Ardea*, 68, 31-52.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology*, 18, 244-256.
- Green, R. F. 1984. Stopping rules for optimal foragers. *American Naturalist*, 123, 30-40.
- Hara, T. J. In Press. The role of olfaction in fish behaviour. In: *The Behaviour of Teleost Fishes*. Ed. by T. J. Pitcher. Beckenham: Croom Helm.
- Hardin, G. 1968. The tragedy of the commons. *Science*, 162, 1243-1248.
- Harley, C. B. 1981. Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89, 611-633.
- Harper, D. G. C. 1982. Competitive foraging in mallards: "ideal free" ducks. *Animal Behaviour*, 30, 575-584.

- Hart, P. J. B. In Press. Foraging in teleost fish. In: *The Behaviour of Teleost Fish*. Ed. by T. J. Pitcher. Beckenham: Croom Helm.
- Hartley, P. H. T. 1948. Food and feeding relationships in a community of fresh-water fishes. *Journal of Animal Ecology*, 17, 1-14.
- Hull, C. H. & Nie, N. H. 1981. *SPSS Update 7-9*. New York: McGraw Hill.
- Hutchinson, G. E. 1939. Ecological observations on the fishes of Kashmir and Indian Tibet. *Ecological Monographs*, 9, 145-182.
- Hyslop, E. J. 1981. The biology of the stone loach *Noemacheilus barbatulus* (L. 1758) and other small fish species in the River Ouzel. Ph.D. Thesis: The Open University.
- Kenward, R. E. 1978. Hawks and doves: attack success and selection in goshawk flights at wood pigeons. *Journal of Animal Ecology*, 47, 449-466.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. In: *Behavioural Ecology: An Evolutionary Approach*. Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.
- Krebs, J. R. & Cowie, R. J. 1976. Foraging strategies in birds. *Ardea*, 64, 98-116.
- Krebs, J. R., Houston, A. I. & Charnov, E. L. 1981. Some recent developments in optimal foraging. In: *Foraging Behavior*. Ed. by A. C. Kamil & J. D. Sargent. New York: Garland STPM Press.
- Krebs, J. R., Kacelnik, A. & Taylor, P. J. 1978. Optimal sampling by foraging birds: an experiment with great tits (*Parus major*). *Nature*, 275, 27-31.
- Krebs, J. R., MacRoberts, M. H. & Cullen, J. M. 1972. Flocking and feeding in the great tit *Parus major*- an experimental study. *Ibis*, 114, 507-530.
- Krebs, J. R. & McCleery, R. H. 1984. Optimization in behavioural ecology. In: *Behavioural Ecology: An Evolutionary Approach* (2nd. edn.). Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.
- Krebs, J. R., Ryan, J. & Charnov, E. L. 1974. Hunting by expectation of optimal foraging? A study of patch use by chickadees. *Animal Behaviour*, 22, 953-964.
- Krebs, J. R., Stephens, D. W. & Sutherland, W. J. 1983. Perspectives in optimal foraging. In: *Perspectives in Ornithology*. Ed. by G. A. Clark & A. H. Bush. New York: Cambridge University Press.

- Lehner, P. N. 1979. *Handbook of Ethological Methods*. New York: Garland STPM Press.
- Lekander, B. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. *Acta Zoologica*, 30, 1-131.
- Lendrem, D. 1983. Predation risk and vigilance in the blue tit. *Behavioral Ecology and Sociobiology*, 13, 9-13.
- MacArthur, R. & Pianka, E. 1966. On optimal use of a patchy environment. *American Naturalist*, 100, 603-609.
- Magurran, A. E. 1984. Gregarious goldfish. *New Scientist* 9/8/1984, 32-33.
- Magurran, A. E., Oulton, W. J. & Pitcher, T. J. 1985. Vigilant behaviour and shoal size in minnows. *Zeitschrift fur Tierpsychologie*, 67, 167-178.
- Magurran, A. E. & Pitcher, T. J. 1983. Foraging, timidity and shoal size in minnows and goldfish. *Behavioral Ecology and Sociobiology*, 12, 147-152.
- Maitland, P. S. 1965. The feeding relationships of salmon, trout, minnows, stone loach and three-spined sticklebacks in the River Endrick, Scotland. *Journal of Animal Ecology*, 34, 109-133.
- Maynard Smith, J. 1972. *On Evolution*. Edinburgh: Edinburgh University Press.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- McFarland, D. J. & Houston, A. I. 1981. *Quantitative Ethology*. London: Pitman.
- McNair, J. N. 1982. Optimal giving up times and the marginal value theorem. *American Naturalist*, 119, 511-529.
- McNair, J. N. 1983. A class of patch use strategies. *American Zoologist*, 23, 303-313.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology*, 21, 269-288.
- McNamara, J. & Houston, A. 1985. A simple model of information use in the exploitation of patchily distributed prey. *Animal Behaviour*, 33, 553-560.
- Milinski, M. 1979. An evolutionarily stable feeding strategy in sticklebacks. *Zeitschrift fur Tierpsychologie*, 51, 36-40.
- Milinski, M. 1984. Competitive resource sharing: an experimental test of a learning rule for ESSs. *Animal Behaviour*, 32, 233-242.

- Milinski, M. In Press. Risk of predation taken by parasitised sticklebacks under competition for food. *Behaviour*.
- Milinski, M. & Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*). *Nature*, 275, 642-644.
- Munger, J. C. 1984. Optimal foraging? Patch use by horned lizards (Iguanidae: *Phrynosoma*). *American Naturalist*, 123, 654-680.
- Neill, S. R. St.J. & Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopod and fish predators. *Journal of the Zoological Society of London*, 172, 549-569.
- Neveu, A. 1981. Rythme alimentaire et relations trophiques chez l'anguille (*Anguilla anguilla* L.), la loche franche (*Nemacheilus barbatulus* L.), le vairon (*Phoxinus phoxinus* L.) et le goujon (*Gobio gobio* L.) dans des conditions naturelles. *Bulletin. Centre d'Etudes et de Recherches Scientifiques (Biarritz)*, 13, 431-444.
- Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. *Theoretical Population Biology*, 12, 263-285.
- O'Connor, R. J. & Brown, R. A. 1977. Prey depletion and foraging strategy in the oystercatcher (*Haematopus ostralegus*). *Oecologia*, 27, 75-92.
- Parker, G. A. 1970. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). II. The fertilisation rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *Journal of Animal Ecology*, 39, 205-228.
- Parker, G. A. 1974. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IX. Spatial distribution of fertilisation rates and evolution of male search strategy within the reproductive area. *Evolution*, 28, 93-108.
- Parker, G. A. 1978. Searching for mates. In: *Behavioural Ecology: An Evolutionary Approach*. Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.
- Parker, G. A. 1984. Evolutionarily stable strategies. In: *Behavioural Ecology: An Evolutionary Approach* (2nd. edn.). Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.

- Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. In: *Behavioural Ecology*. Ed. by R. M. Sibly & R. H. Smith. Oxford: Blackwell.
- Perrin, J. F. 1980. Structure et fonctionnement des ecosystèmes du Haut-Rhône Français. 14 - Etude des préférences alimentaires de la loche franche (*Noemacheilus barbatulus* L.) par une méthode des points modifiée. *Hydrobiologia*, 71, 217-224.
- Pitcher, T. J. 1983. Heuristic definitions of fish schooling behaviour. *Animal Behaviour*, 31, 611-613.
- Pitcher, T. J. In Press. The functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes*. Ed. by T. J. Pitcher. Beckenham: Croom Helm.
- Pitcher, T. J. & Magurran, A. E. 1983. Shoal size, patch profitability and information exchange in foraging goldfish. *Animal Behaviour*, 31, 546-555.
- Pitcher, T. J., Magurran, A. E. & Allan, J. R. 1983. Shifts of behaviour with shoal size in Cyprinids. *Proceedings of the British Freshwater Fisheries Conference*, 3, 220-228.
- Pitcher, T. J., Magurran, A. E. & Winfield, I. J. 1982. Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, 10, 149-151.
- Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, 38, 419-422.
- Pulliam, H. R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: *Behavioural Ecology: An Evolutionary Approach* (2nd. edn.). Ed. by J. R. Krebs & N. B. Davies. Oxford: Blackwell.
- Pulliam, H. R., Pyke, G. H. & Caraco, T. 1982. The scanning behaviour of Juncos: a game theoretical approach. *Journal of Theoretical Biology*, 95, 89-103.
- Pyke, G. H. 1978. Optimal foraging in hummingbirds: testing the marginal value theorem. *American Zoologist*, 18, 739-752.
- Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52, 137-154.
- Regelmann, K. 1984. Competitive resource sharing: a simulation model. *Animal Behaviour*, 32, 226-232.
- Rohlf, F. J. & Sokal, R. R. 1981. *Statistical Tables* (2nd. edn.). San Francisco: Freeman.

- Sauvonsaari, J. 1971. Biology of the stone loach *Nemacheilus barbatula* L. in the lakes Paijanne and Paikanevesi, Southern Finland. *Annales Zoologici Fennici*, 8, 187-193.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369-404.
- Seghers, B. H. 1981. Facultative schooling behaviour in the spottail shiner (*Notropis hudsonius*): possible costs and benefits. *Environmental Biology of Fishes*, 6, 21-24.
- Sibly, R. M. 1983. Optimal group size is unstable. *Animal Behaviour*, 31, 947-948.
- Sih, A. 1980. Optimal foraging: can foragers balance two conflicting demands. *Science*, 210, 1041-1043.
- Silliman, J., Scott Mills, G. & Alden, S. 1977. Effect of flock size on foraging activity in wintering sanderlings. *Wilson Bulletin*, 89, 434-438.
- Smith, J. N. M. & Sweatman, H. P. A. 1974. Food searching behaviour of titmice in patchy environments. *Ecology*, 55, 1216-1232.
- Smyly, W. J. P. 1955. On the biology of the stone loach *Nemacheilus barbatula* (L.). *Journal of Animal Ecology*, 24, 167-186.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry* (2nd. edn.). San Francisco: Freeman.
- Sterba, G. 1958. Die schmerlenartigen (Cobitidae). In: R. Demoll & H. N. Mayer. *Handbuch der Binnenfischerei Mitteleuropas*, 3(9), 201-231.
- Street, N. E. & Hart, P. J. B. (In Press). Group size and patch location by the stoneloach (*Noemacheilus barbatulus*)- a non-visually foraging predator. *Journal of Fish Biology*.
- Street, N. E., Magurran, A. E. & Pitcher, T. J. 1984. The effects of increasing group size on handling time in goldfish, *Carassius auratus* L.. *Journal of Fish Biology*, 25, 561-566.
- Studd, M., Montgomerie, R. D. & Robertson, R. J. 1983. Group size and predator surveillance in foraging house sparrows *Passer domesticus*. *Canadian Journal of Zoology*, 61, 226-231.
- Sutherland, W. J. 1983. Aggregation and the "ideal free" distribution. *Journal of Animal Ecology*, 52, 821-828.
- Sutherland, W. J. & Parker, G. A. 1985. Distribution of unequal competitors. In: *Behavioural Ecology*. Ed. by R. M. Sibly & R. H. Smith. Oxford: Blackwell.

- Weihs, D. 1973. Hydromechanics and fish schooling. *Nature*, 241, 290-291.
- Welton, J. S., Mills, C. A. & Rendle, E. L. 1983. Food and habitat partitioning in two small benthic fishes, *Noemacheilus barbatulus* (L). and *Cottus gobio* L.. *Archiv fur Hydrobiologie*, 97, 434-454.
- Werner, E. E. & Mittelbach, G. G. 1981. Optimal foraging: field tests of diet choice and habitat switching. *American Zoologist*, 21, 813-829.
- Wheeler, A. 1978. *Key to the Fishes of Northern Europe*. London: Frederick Warne.
- Whitham, T. G. 1979. Territorial behaviour of *Pemphigus* gall aphids. *Nature*, 279, 324-325.
- Whitham, T. G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. *American Naturalist*, 115, 449-466.
- Zach, R. & Falls, J. B. 1976. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment. *Canadian Journal of Zoology*, 54, 1863-1879.
- Zwarts, L. 1974. *Vogels van het Brakke Getijgebeid*. Amsterdam.
- Zwarts, L. 1976. Density-related processes in feeding dispersion and feeding activity of teal (*Anas crecca*). *Ardea*, 64, 192-209.
- Zwarts, L. 1978. Intra- and inter-specific competition for space in a one-prey situation. Berlin: International Ornithological Congress.

Group size and foraging in stoneloach, *Noemacheilus barbatulus*,
by Nigel E. Street.

The effects of group size on aspects of stoneloach foraging behaviour were examined in laboratory experiments. Fish were observed under dark conditions, using infra red illumination and video equipment. Experiments were timed to coincide with the stoneloach's natural time of maximum activity, immediately after a period of artificially simulated dusk.

Individual stoneloach located a concealed food source more rapidly when group size was increased from one to five fish. Large quantitative differences were observed between fish, and those which were slow to locate food when alone remained poor when conspecifics were present.

Over a 900 sec period, individuals in groups of five fish spent a greater proportion of available time searching, and appeared to sample the environment more, when compared with individuals in groups of only two. An increase in sampling may have counteracted the observed reduction in the number of feeding attempts by the fish in the larger groups, which resulted from the increased emphasis on searching.

Groups of both six and twelve fish, foraging in tanks comprising two feeding areas each containing a patch, and a central area where no food was available, distributed themselves roughly in accordance with the predictions of an ideal free distribution when patches were equally profitable. When the patches differed in profitability in a ratio of either 2:1 or 5:1, the number of fish found in the low profitability area was as predicted. However, the number found in the high profitability area fell below that predicted, due to the presence of some individuals in the central area of the tanks. It is suggested that the latter individuals were found in the central area as a result of non-aggressive interference between individuals in the high profitability area.

Finally, the marginal value theorem was used to predict the optimal patch residence time. The prediction was met in experimental tests at a group size of one, but at group sizes of two or five fish the observed time was significantly lower than that predicted.