

Estimation of population densities
of carabid beetles in cereal crops

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To Hilary

Poor fool, with all this sweated lore,
I stand no wiser than I was before.
Master and Doctor are my titles;
For ten years now without repose,
I've held my erudite recitals
And led my pupils by the nose.
And round we go on crooked ways or straight,
And well I know that ignorance is our fate,
And this I hate.

Goethe: Faust I

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CHAPTER 1

Introduction

Beetles of the family Carabidae have been studied extensively by entomologists and have proved interesting objects of study in all areas of biology (Den Boer, 1986). It is the largest of all insect families with an estimated 40,000 species world-wide (Basilewsky, 1972). Carabids are active epigeic insects particularly well adapted to a cursorial existence and with predominantly soil-dwelling immature stages. Much of the adult life is spent on the soil surface where the beetles spend time searching for food and individuals of the opposite sex. They have a worldwide distribution and are common in most terrestrial habitats. The systematics of the family has been studied thoroughly in Britain (Lindroth, 1974) and few problems are experienced in identifying individual beetles to the level of species.

Several general studies have been undertaken in cereal crops including Rivard (1965), Den Boer (1977), Jones (1979), Luff (1982a) and Ekbom & Witkelius (1985). Most species are polyphagous predators (Forbes, 1881) and there are many examples in the literature where species have been shown to feed on pests of man and his crops: Burgess & Collins (1911) (larvae of *Operophtera brumata* (L.)); Stage & Yates (1939) (the eggs of *Aedes* mosquitoes); Fox & MacLellan (1956) (*Agriotes spurator* (L.)); Dempster et al. (1959) (the pupal stage of *Phytodecta olivacea* (Forster)); Coaker & Williams (1963) (larvae of *Delia brassicae* (Hoff.)); Karg (1970) (*Leptinotarsa decemlineata* Say); Jones (1975) (*Delia coarctica* (Hendle)); East (1974) (pupae of *Operophtera brumata* (L.)); Parry & Pendleberry (1986) (collembolan

and tipulid pests in hardwood nurseries). Only rarely have species been shown to have detrimental effects on crops (Whitney, 1938; Morrison, 1941; Dick & Johnson, 1958; Briggs, 1965) and they are now generally considered as beneficial arthropods in most agricultural-pest situations.

Several species which inhabit the arable ecosystem have been shown to be aphidophagous (Potts & Vickerman, 1974; 1975; Sunderland, 1975; Dunning et al. 1975; Vickerman & Sunderland, 1975; De Clerq & Pietraszko, 1983; Holmes, 1984; Chambers et al., 1986; Sopp & Chiverton, 1987). This is of importance considering the pest status of aphids in many cereal crops (Vickerman & Wratten, 1979). Not surprisingly, many workers now regard some species as potential biological control agents. The main disadvantage is the difficulty encountered in breeding large numbers for inoculation or inundation as part of integrated pest management strategies.

It is known that aphid infestations can affect the quality of a crop, for example the baking quality of wheat flour is inversely proportional to the cumulative aphid index (Lee et al., 1982). Entwistle & Dixon (1986; 1987) were able to make short-term forecasts of peak population densities of *Sitobion avenae* and of wheat yield loss from the number of aphids per tiller and the rate of increase over the previous days. This means that pesticides need not be used during the early stages of aphid infestation when carabids are capable of controlling pest outbreaks. This is important because many pesticides (and herbicides) have a more detrimental effect on predators than on pests such as aphids which have a relatively short generation time (Freitag & Poulter, 1970; Dempster, 1972; Brown et al., 1983; Matcham & Hawkes, 1985; Shires, 1985)

Hagen et al. (1976) reported that polyphagous predators such as carabids are important in preventing pest outbreaks in monocultures

and Edwards et al. (1979) demonstrated more precisely the role of carabids in restricting the build up of aphid populations in cereals. These findings were supported by Sunderland et al. (1980); Scheller (1984) and Chiverton (1987) who demonstrated that carabids consumed individuals of *Rhopalosiphum padi* during the aphid's pre-peak period in spring barley. In addition to this Sopp et al. (1987) demonstrated that a higher proportion of the aphid population was on the soil surface when densities were lowest on the plants i.e. during the early stages of aphid infestation (the extent to which aphids fall to the ground is important since only a few species of Carabidae such as *Demetrias atricapillus* are able to climb plant stems (Vickerman & Sunderland, 1975)).

In recent years a considerable body of detailed research has been published on the aphidophagous capacity of carabids in the agroecosystem. Sunderland & Vickerman (1980) determined the percentage of individuals collected from the field which contained aphid remains. These include *Notiophilus biguttatus* (19%; n=656), *Pterostichus melanarius* (17%; n=937) and *Bembidion lampros* (9%; n=1641). Similar results were obtained by Chiverton (1987) who also studied *Bembidion quadrimaculatum* (15.1%; n=470) and *Pterostichus niger* (55.2%; n=29). Other workers have rank-ordered species according to aphidophagous capacity (Edwards & George, 1977; Edwards et al., 1978) and more detailed experiments on consumption capacity have recently been carried out in the laboratory (Sopp & Wratten, 1986).

Although not specific predators, they are advantageous in that they are likely to remain in a crop when pest populations are low (e.g. Luff (1982a) found little fluctuation in population density from year to year unless the pattern of cultivation altered) and 'switch' between pest species according to availability. The

disadvantage is that they are unlikely to respond rapidly to a pest outbreak due to the longer generation time relative to pest species such as aphids.

In a review of other literature, Hance (1987) argues that new agricultural practices such as the decrease in the number of farmers rotating crops or leaving fields fallow is thought to have contributed to the decline in the numbers of epigeic arthropods, especially beneficial predators. This is not the only explanation for the decrease. The problems associated with the use of pesticides, and particularly the greater susceptibility of predators as opposed to pest species, are well documented. Long term sampling in cereals in West Sussex (1970–1979) led Vickerman (1980) to report a significant decline in numbers of 45% of non-pest species as opposed to 5% of pest species. Pesticides were thought to be responsible for this difference. Such problems will continue whilst the Pesticides Safety Precaution Scheme remains voluntary (about 80 chemicals are still approved for use in cereals alone (Vickerman, 1980)). In the philosophy of Integrated Pest Management it should be our aim to increase the numbers of indigenous predators and decrease the use of chemicals but it seems unlikely that this can be achieved without legislation. Sunderland et al. (1984) identified 390 species of polyphagous predators in UK cereal crops, many of which were Carabidae, and so the potential is clearly there for a reversal of current trends.

Due to their relatively high mobility the beetles are readily captured by pitfall traps. The invention of this sampling technique has been attributed to various authors but it can be traced back to Barber (1931) who used the method to capture cavernicolous insects. Hence the traps are occasionally referred to as "Barber traps". This

method has now come into widespread use for sampling populations of surface-active arthropods - especially Carabidae and Araneae. Its use has been the foundation of much experimental ecological research and has widened our knowledge of the habitat distribution pattern and long term population fluctuations of many species of Carabidae.

Many modifications to the basic design of the pitfall trap have been published: Heydemann (1956;1958); Morrill (1975); Houseweart et al. (1979); Reeves (1980); De Los Santos et al. (1982); Durkis (1982); Bostanian et al. (1983) and Epstein & Kulman (1984). These modifications were aimed at increasing the capturing efficiency of traps. Essentially, the technique involves the placement of collecting vessels into the ground so that the upper rim is flush with the soil surface. In theory, any moving animal reaching the perimeter of such a trap will fall in and thus be captured and remain in the preservative fluid in the bottom of the trap. The technique is therefore low on effort from the point of view of the scientist since the collection of data relies on the activity of the insects themselves.

It has been demonstrated (Briggs,1961; Lesiewicz et al., 1983; Desender et al., 1985 and others) that the number of individuals of any one species captured by a pitfall trap does not correlate with the actual abundance of the species in the same locality. An explanation for this discrepancy is that the number of animals captured depends not only upon the abundance of a species but also on the activity of individuals. Only Dubrovskaya (1970) found a significant correlation between the two and her results are difficult to explain in the light of other research.

Hence pitfall traps cannot be used for quantitative estimations of absolute abundance of any one species. Similarly, attempts to make relative population density estimates in a comparative way across the

family are also unsuccessful because activity rates differ interspecifically i.e. individuals of some species will encounter, and be captured by, traps more readily than others. Intraspecific inter-habitat comparisons of pitfall data can give comparable estimates of relative population density if it is assumed that beetles encounter traps at an equal rate in the different habitats. For this assumption to be realised the habitats must be similar (see below).

The problem of the usefulness of pitfall traps was partially resolved by suggesting that the number of individuals captured by a pitfall trap should be referred to as the 'activity density index' (Heydemann, 1953) or the 'activity abundance index' (Tretzel, 1955) for any one species. In other words, pitfall-trap data is represented by a single parameter which is made up of two inseparable components of the species' phenology - the mean activity rate and the absolute abundance of individuals in the proximity of the trap. This too has its drawbacks, especially when inter-habitat comparisons are being made, since habitat is likely to influence individual activity rates. Also, within the same habitat, inter-specific effects of changes in climate, for example, will not necessarily be equal with respect to activity.

Even so, activity abundance is not without ecological significance since carabids have been identified as beneficial insects in the agroecosystem (see p.2) and Thiele (1977) suggests that this parameter can be used as a measure of this effectiveness since predatory carabid beetles must search for relatively sedentary prey such as aphids. It has been suggested that more active beetles should encounter such prey more frequently and hence be more capable

of suppressing their outbreak. Thus seen, it is a measure of the role of a species in the ecosystem (Thiele op. cit.). However, the relationship between predator activity and prey consumption is unlikely to be as straightforward as this since activity is only one of many components of a predator's hunting strategy: many insect predators rely on highly developed visual and chemical methods of prey detection, on camouflage etc.

Techniques for estimating absolute population density do exist, but each has its associated problems: using quadrats to determine absolute abundance is inefficient for Carabidae due to their low population density. The use of the mark-release-recapture technique is also limited by low population density (necessary to provide sufficient recapture data), and the need to satisfy the various assumptions of the theoretical models. Also, in most mark-release-recapture studies, it is necessary to keep alive individuals which are captured so that they can subsequently be released. When using pitfall traps in this way therefore, no preservative fluid can be used in the base of the trap. As a consequence, inter- and intra-specific predation within the pitfall trap between observations is an additional problem. The investigation of the quantitative distribution of carabids has therefore been limited by the availability of a suitable technique.

For want of a better alternative, and due to the difficulty of applying theoretical models such as the one proposed by Jansen & Metz (1977 see below) to the field situation, the activity abundance index has now been generally adopted by carabidologists as a means of quantifying pitfall-trap data within a habitat, and for making intra-specific inter-habitat comparisons of relative population densities.

Many carabids of the agroecosystem have already been rank-ordered according to their aphidophagous capacity and this takes into account the role of activity in determining their relative importance as aphid predators. The activity abundance index is therefore of limited use in this respect. What is still required is a suitable technique for the measurement of their absolute, or even relative abundance, so that, by combining rank with abundance, their true potential as aphid predators in any one situation can be realised.

One approach might be to quantify activity in some way and thus separate it from abundance for each species. It would then be possible to derive the abundance data from pitfall-trap data to at least give a relative estimate of interspecific population abundances. However, before this can be attempted, there is one factor which has until now been ignored - the potential for individual beetles to respond negatively upon encountering a pitfall trap. If this potential differs interspecifically then the term activity abundance, when used to describe pitfall data, becomes misleading: the number of beetles captured by a trap would not only depend on the abundance and activity of individuals within a species, but also upon the response of beetles upon encountering a trap. I suggest that where this response is a negative one (the beetle is not captured by the trap) then the term 'pitfall trap avoidance' should be used.

Greenslade (1961) studied a similar concept - pitfall trap efficiency, and defined this as the capacity of a particular trap to capture beetles. This capacity, he suggested, was determined by several factors including the texture of the vegetation immediately surrounding the trap, the intrinsic properties of the trap used and the behaviour of the beetles themselves. No attempt was made to

quantify the last or to separate the main contributory factors.

Mitchell (1963) proposed the following equation to allow relative population density to be calculated from pitfall trap captures:

$$C \propto f(AN)$$

where C=number of individuals captured, A=activity and N=the population density. He suggested that f would be some complex mathematical function.

In a theoretical study, Jansen & Metz (1979) recognized four factors which affect the number of individuals of a species captured by a trap. These are:

1. Population density
2. Movement
3. Pitfall boundary - 'adsorptiveness'
4. Outer area boundary - probability of adsorption is the extent to which beetles can penetrate this boundary.

Here pitfall adsorptiveness is similar to pitfall trap efficiency and is thus dependent upon the surrounding habitat.

Kudrin (1971) compared the capture efficiency of rough and smooth sided traps but did not make any interspecific comparisons with respect to one type of trap. In laboratory and field studies, Luff (1975) demonstrated quantitatively that beetles do avoid pitfall traps but still referred to this as "capture efficiency" (p.347) thus placing the responsibility on the trap rather than on the beetles. He allowed 100 individuals of each of 6 species to encounter traps in the laboratory and found that the efficiency ranged from 53.3 to 80%

depending on the type of trap and species. In addition to this he found that small traps in the field were more efficient at capturing small species than were large traps and that the largest species were caught poorly by nearly all types of trap tested. The significance of these results will be discussed further in the light of results presented in Chapter 4.

Only two other references to pitfall trap avoidance could be found in the literature but in each case no quantitative assessment was made. Sunderland & Vickerman (1980) refer to what in this thesis is called pitfall trap avoidance by stating that pitfalls discriminate against species such as *Demetrias atricapillus* and *Tachyporus hypnorum* (Staphylinidae) "which are poorly represented in pitfalls even when very numerous in ground-search samples This could be due to variations in avoidance behaviour causing differential catching of carabid species in pitfalls." (p.394). Lesiewicz et al. (1983) referred indirectly to the parameter by describing pitfalls as behaviourally sensitive instruments. The majority of papers published simply state that the number of individuals captured by pitfall traps is determined only by population density and activity.

Thus the two concepts pitfall-trap efficiency (Greenslade, 1961) and pitfall-trap avoidance are subtly different. The former depends on three factors, namely the state of the trap, the effect of the habitat and the behaviour of the beetle, whereas the latter, as defined in this study, considers only the behaviour of the beetle upon encountering a trap.

If identical traps are used, and care is taken to position them correctly in the soil, then the type of response of a beetle should depend only upon its behaviour immediately before encountering a trap

and not on the intrinsic properties of the traps themselves. Only if the beetle's behaviour (other than its activity) prior to an encounter with a trap is determined by the vegetation, can it be said that the habitat influences the response of the beetle to the pitfall trap. In a monoculture such as a wheat or barley crop, differences between traps with respect to the surrounding vegetation and soil will be minimal, and the texture of the vegetation and soil should only determine the rate at which encounters with traps take place and not the type of response which subsequently follows. In such a situation, the response of a beetle will be determined by its activity rate prior to an encounter with a trap, by its behaviour upon encountering the trap perimeter, or by both.

Ecological investigations of avoidance behaviour by invertebrates usually involve some sort of response to naturally occurring substances which have a potentially detrimental effect upon the animal e.g. a toxicant. The first such study of avoidance behaviour by a macroinvertebrate was by Costa (1966) working on *Gammarus pulex* (L.). Olla (1980) discussed such behaviour (with respect to a toxic substance in the marine environment) in some detail. He isolated three distinguishable facets of this type of behaviour:

1. Sensing an environmental change
2. 'Recognising' the change as being adverse
3. Responding accordingly

and that if any one component fails, the consequences would be fatal.

There is clearly the capacity for the selection of such behaviour where animals come into contact with potentially toxic

substances. Hardwick (1985) studied the response of aquatic gammarids to various concentrations of zinc and also discussed the significance of avoidance behaviour. She concluded (p.98) that "A response is successful if it removes or lessens the effect of a toxicant, thereby reducing the probability of death or energetic cost of compensatory responses".

The extent to which such a statement can be applied to beetles and pitfall traps will be discussed in Chapter 4 in more detail, but it is possible to relate the significance of artificial objects such as pitfall traps to the niche of the carabid beetle through evolutionary history by analogy. The potentially detrimental effects of an equivalent drop into a body of water in the beetle's habitat would perhaps evoke a similar response, and we could assume that such behaviour has been, and is still being, selected for. One rarely observes beetles falling off the edge of a stone or the tip of a leaf, and it is reasonable to assume that given sufficient time to respond to an encounter with the perimeter of a pitfall trap, the response would be not to fall into the trap i.e. the beetle would avoid the trap.

We are clearly not in a position to assume that the behaviour of a beetle, when encountering the perimeter of a trap, has been directly selected for, but the situation is analagous to others both now and in the evolutionary history of its ancestors.

One aim of the present study was to investigate the response of individuals of several species of Carabidae to pitfall traps of a particular uniform design, and to determine what factors influence the type of response observed and the frequency with which a particular response occurs. Studies were carried out both in the laboratory and in the field and involved 10 common species of Carabidae which occur in arable land. Field work was carried out in

as uniform a habitat as possible (an arable field) so that the minimum difference between traps with respect to habitat resistance was experienced.

Several workers have studied the effects of various preservatives which are used in pitfall traps. Such solutions are used to prevent predation between individual animals within the trap and also to minimise the chance of escape. The apparent attractive properties of formaldehyde have been pointed out by Luff (1968), Skuhavy (1970) Greenslade & Greenslade, (1971) and Adis (1974). However, it is uncertain as to what is the exact cause of the bias (with respect to the number of individuals captured) towards traps in the field containing formaldehyde when compared with traps containing water or no preservative. The studies of Petruska (1969) show that beetles are able to escape at a very low frequency from some traps which contain 4% formaldehyde. It may be that beetles are less likely to escape from traps containing formaldehyde due to its greater toxicity. Indeed, Skuhavy (1970) demonstrated that in such traps, the catch showed a significant bias towards females and he suggested that this may be a reflection of the greater capacity of males, which often have bristles on the anterior tarsi, to escape from a trap. Adis & Kramer (1975) convincingly demonstrated that one species, *Carabus problematicus*, is attracted to formaldehyde, although only in the spring. It may be that the differences observed are a consequence of both the attractive capacity of formaldehyde (due possibly to the erroneous perception of the aldehyde as a pheromone) and its greater toxicity, and therefore power of retention of captured beetles.

Consequently, we have yet another parameter with which to contend - if species are differentially attracted to pitfall traps,

and if the degree of attractiveness fluctuates temporally, then this must also be accounted for if the sampling technique is to be used in quantitative studies. This problem is also tackled in the present study.

In addition to the study of the avoidance of pitfall traps, an attempt is made to quantify the activity of beetles in the field using individuals of five of the species studied with respect to pitfall-trap avoidance. The relative motility of carabids has been studied in the field by Heydemann (1957), Skuhrahy (1957a), Kirchner (1960), Grum (1971) and Baars (1979a;b) and in the laboratory by Thiele (1977) and Brunsting (1983). Except for the results of Heydemann (*op. cit.*), the smallest time interval between observations in the field studies quoted was 24 hours, and so the studies are essentially estimates of the dispersal power (as measured in a straight line from the original point of release) rather than the actual velocity of beetles.

The work cited by Thiele (1977) is more detailed in that constant observation over a distance of 30cm in the laboratory allows the calculation of mean velocities, but he points out the dangers of extrapolation from such results. However, comparable speeds were obtained by Heydemann (1957) in field studies.

In the present study (see Chapter 5) beetles were observed continually in the field for periods of 15 minutes, and their pattern of locomotion recorded. To my knowledge, this is the first such study of activity in the field.

Finally, absolute abundance estimates for several species were made using both quadrat sampling and a mark-release-recapture study. This work on population density is presented in Chapter 3.

The overall aim of this study, although ambitious, was to input data on activity to a computer simulation program. The simulation results (in terms of the proportion of individuals of each species encountering traps), it is argued, could then be used along with data on the avoidance rate of each species to modify pitfall trap data from the field. The results could then be compared with absolute population estimates from the same study site to determine the success of such an approach. If successful, the method would allow one to arrive at an estimate of relative population densities for a group of species by simply modifying pitfall-trap data according to these two parameters: activity and avoidance.

If the estimated relative abundances of several species can be predicted from the model then it would only be necessary to estimate the absolute abundance of one of these species to be able to predict the absolute abundances of all of the others. The whole approach to the problem of estimating absolute abundances from pitfall-trap data is summarised in Fig. 1.1 on the following page.

If this approach proved unsuccessful, an improved definition of 'activity abundance' through a study of avoidance behaviour in the laboratory and field was within the scope of this study.

CHAPTER 2

The study site, Carabidae and general methods

2.1 Charnwood Lodge: A site for field work and a source of animals for laboratory and field experiments.

Charnwood Lodge Nature Reserve forms part of an extensive area known as Charnwood Forest which runs from the north to northwest of Leicestershire.

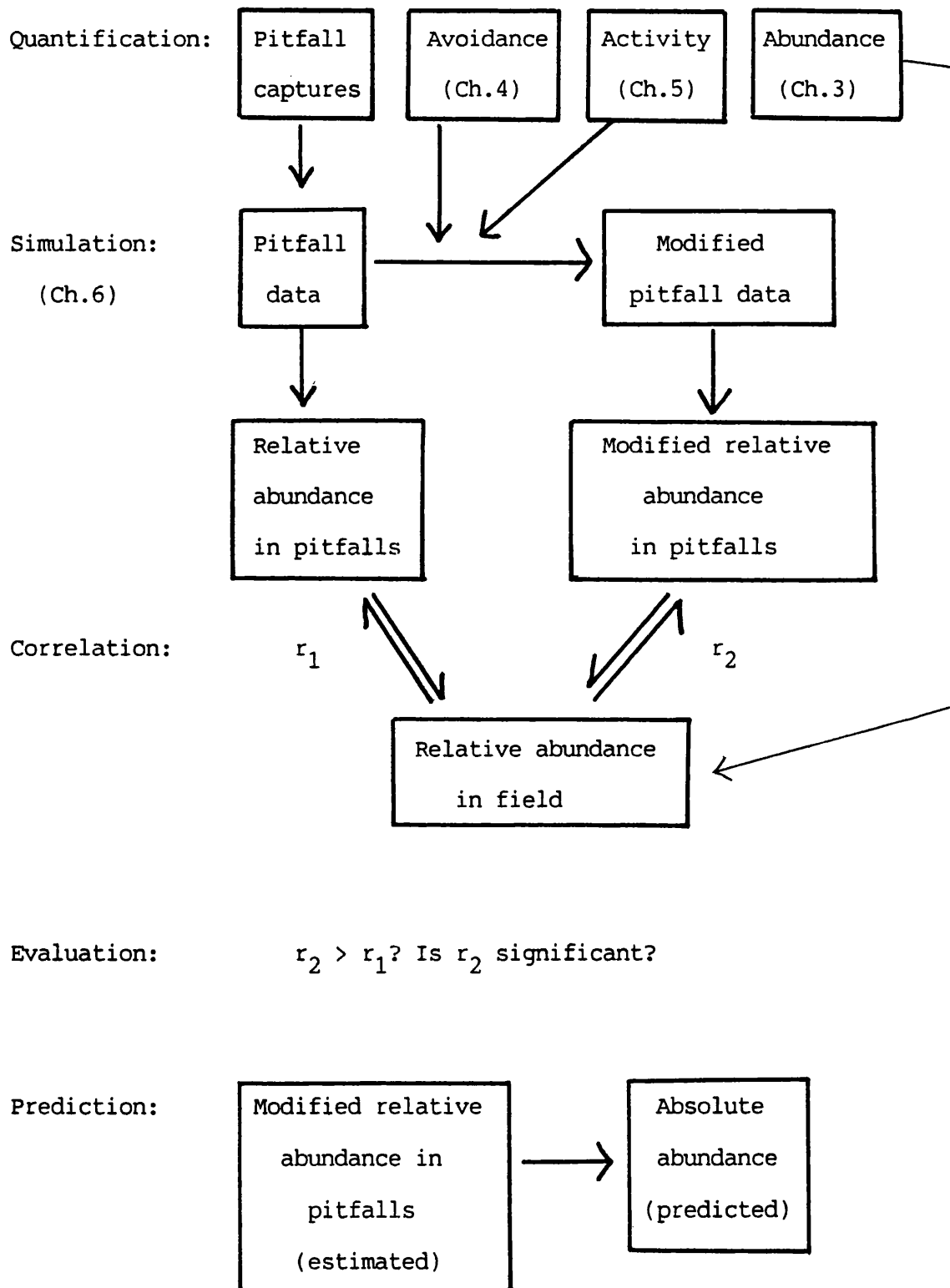
Charnwood Forest is formed upon the most south-easterly outcrop of sileaceous rock in Britain and its whole character can be described as upland both because of the relatively high altitude and the acidic nature of the soil (Ratcliffe & Connolly, 1972). Common and locally restricted vegetation types include dry and wet heath, moorland and rough grazing.

The area occupied by woodland has progressively declined since the proliferation of agricultural practices in the 11th Century to the extent that it now only represents approximately 2% of the land surface of the county. A high proportion of contemporary woodland has been recently felled and replanted, although some natural areas do exist.

More than 80% of the land in Leicestershire is now given over to agriculture with approximately 50% of this being grassland pasture (Evans & Block, 1972). In common with most areas of lowland Britain, much of the arable land is farmed intensively and the pasture improved by the application of fertilizers and selective herbicides.

Charnwood Lodge Nature Reserve was bequeathed to, and is now owned by, the Leicestershire and Rutland Trust for Nature Conservation. It is located in the NW of the county (map reference SK

Fig. 1.1 Summary of main study aims



4615) near the mining town of Coalville, approximately 24 km from the University. It comprises 227 ha of woodland, bracken heath, acid grassland and arable land and most of the Reserve falls under an SSSI designation.

Part of the Reserve is located in one of the highest areas above sea level in Leicestershire (215m) and many of the habitats can be described as upland. *Erica tetralix* L., the cross-leaved heath and *Calluna vulgaris* (L.) Hull, common heather, are typical plant species in some of the grassland habitats and *Empetrum nigrum* L. (crowberry) was present until recently on Timberwood Hill. Curlew and wheatear are also present and so too are some moorland species of Lepidoptera.

Other locally interesting species of angiosperms found on the Reserve include *Anagallis tenella* (L.) L. the Bog Pimpernel and *Scutellaria minor* L. the Lesser Skull-cap. Hydrophilic plants are now encouraged by the conservation of marshy areas but much of the land was drained in the early 19th Century resulting in a prolific spread of bracken over much of the open areas (Bullock & Tobin, 1987). Attempts to rectify this situation include the removal of old drainage pipes, restrictions on drainage operations and the gradual physical removal of bracken stands (the use of chemicals is not permitted on the Reserve).

Drainage was accompanied by afforestation and Gisbornes Gorse, which was planted in the late 19th Century, contains a mixture of species including oak, sycamore, beech, spruce and some exotic specimens.

Other parts of the Reserve are interesting geologically: Marl and other Triassic deposits form the upper stratum of the Earth's crust in this region but outcrops of Precambrian rocks occur on Flat Hill (see map Fig. 2.1).

The Geology and Zoology Departments at Leicester University

maintain a field centre in a converted cottage on the Reserve and part of the agreement upon transfer of the deeds of the land to the Trust was that *bona fide* research students be allowed access to the area. Leow (1980) was the most recent of these and carried out ecological field work on the Staphylinidae of the Reserve. Other than this, the long term operation of pitfall traps by the Zoology Department is the main entomological field work to have been carried out in recent years.

The arable land, which occupies approximately 30% of the area of the Reserve, exists under an agricultural tenancy and is farmed by the tenant, Mr. I. Danvers of High Tor Farm. In addition to this, various rough heathland and grassland areas are subject to short-term grazing letts.

It has been the policy of the farmer, in consultation with the County Trust for Nature Conservation, to abstain from using both organic and inorganic chemicals on arable land within the Reserve and in this sense it differs from most farms in lowland Britain. Very little of the arable land on High Tor Farm is cropped for cereals. The quality of the grain produced does not need to be of a high standard since it is used as a source of food for cattle on the farm. Consequently, the agricultural practices in operation can be described as non-intensive.

The majority of fieldwork was carried out in one of the arable crops. An artificial reservoir, deciduous woodland, rough grassland and pasture surround the field making it a particularly interesting example of the agroecosystem.

The field has an area of 3.44 ha and approximately 85% (686m) of the length of the field boundary (807m) borders grassland. For the remaining 15% (121m), the field borders mixed woodland (See Fig. 2.2). The field is on an incline with a north-south positive gradient

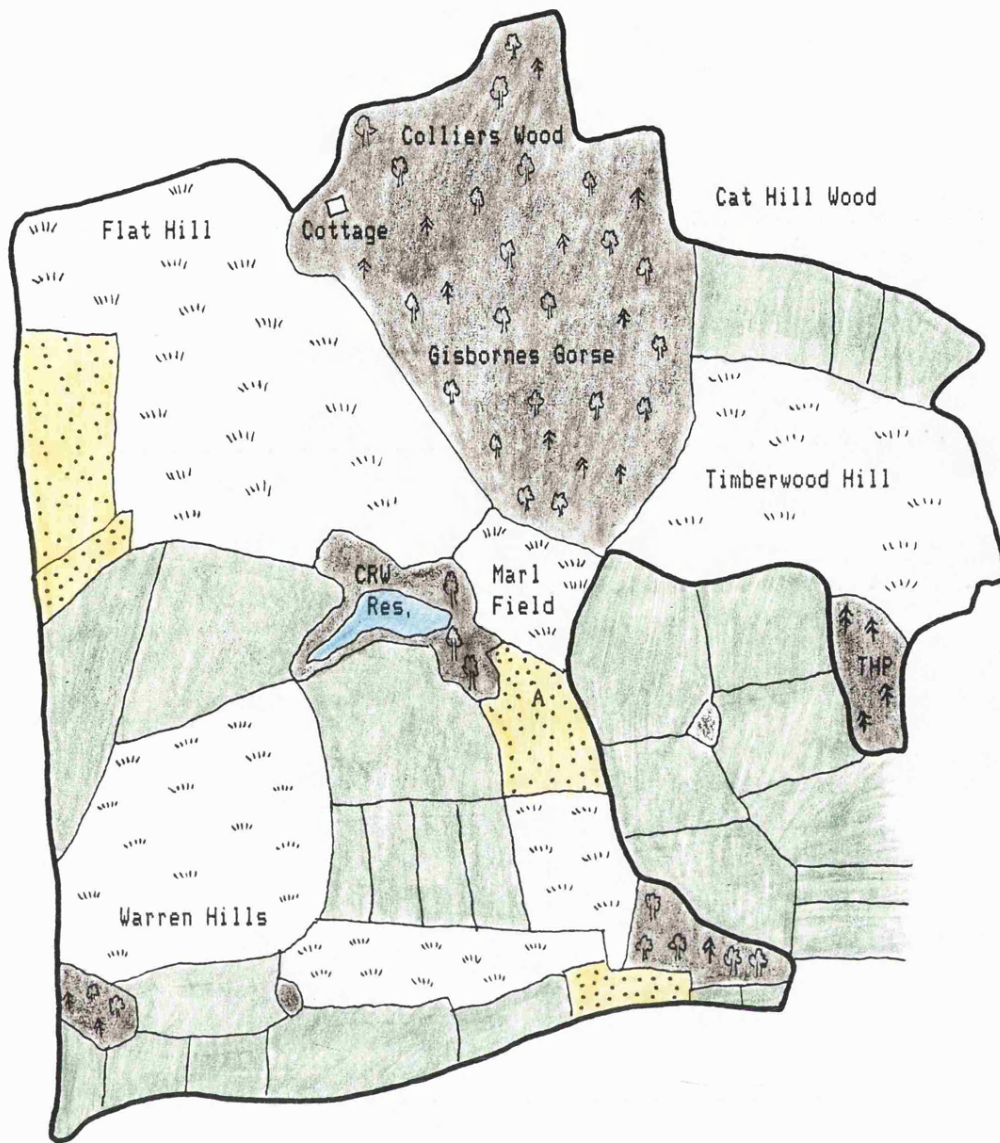


Fig. 2,1 Charnwood Lodge Nature Reserve

250m

- A = Arable study site
 CRW = Colony Reservoir Wood
 THP = Timberwood Hill Plantation
 — = Boundary of Reserve
- | | |
|--|---|
|  = Woodland |  = Arable crops |
|  = Pasture |  = Rough grassland |



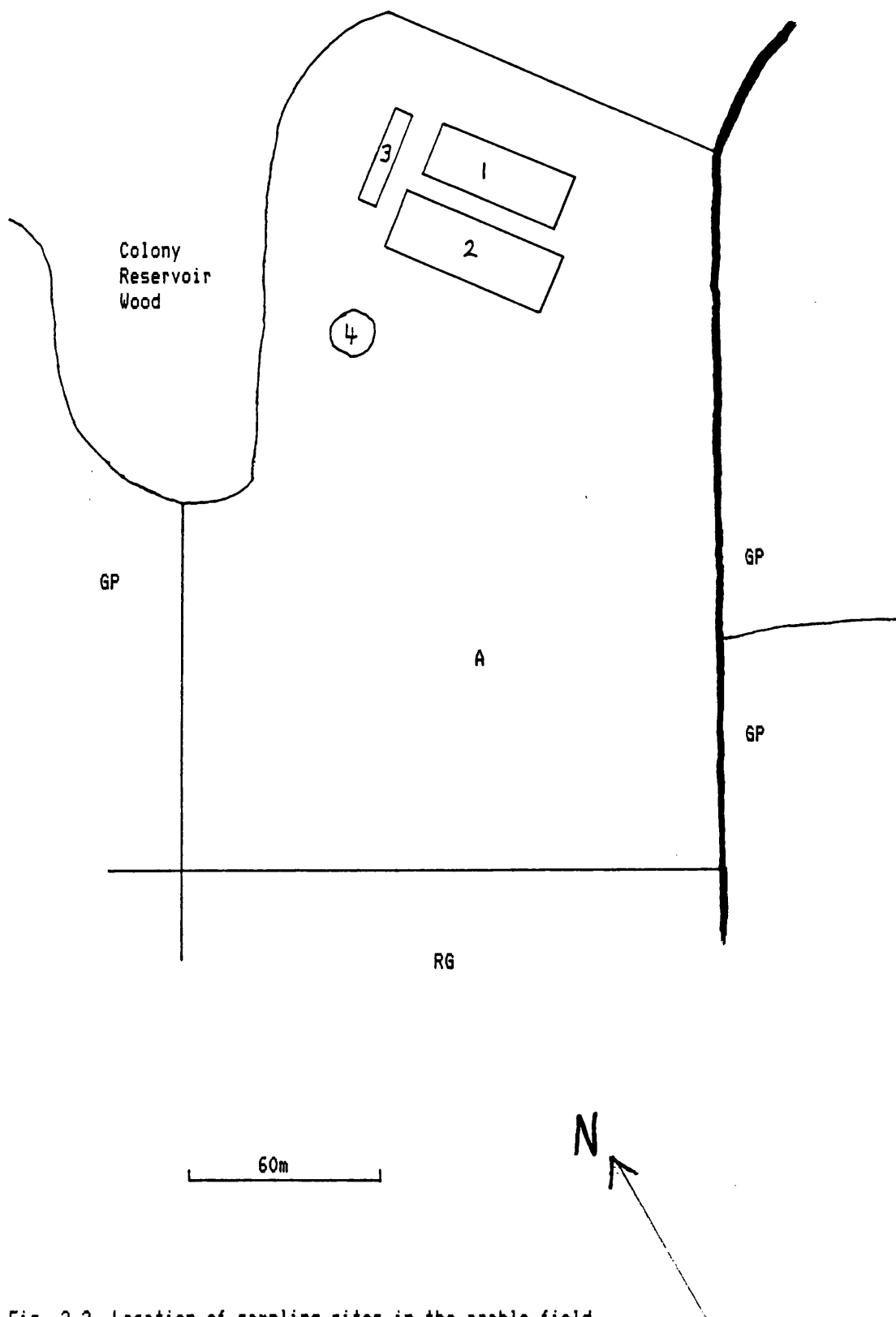


Fig. 2.2 Location of sampling sites in the arable field.

A = Arable crop (the study site)

GP = Grassland pasture

RG = Rough grassland

— = Boundary of the Reserve

1= Main pitfall sampling grid 2= Quadrat sampling grid
3= Mark-release-recapture grid 4= Rocky outcrop



Plate 2.1 Charnwood Cottage - the base for field experiments.



Plate 2.2 View along the southern boundary of the field, looking west.



Plate 2.3 View from the southern boundary of the field, looking north. Colony Reservoir Wood is in the centre. In the right of the photograph Gisbornes Gorse lies beyond Marl Field.

of approximately 4%. After heavy rainfall, the northern end of the field often becomes very boggy.

At the southern end of the field (see Plate 2.1) a large unmanaged hedge, approximately 3m wide, separates the arable field from rough grassland (used for hay production throughout the study period). The dominant species occurring in the hedge is *Crataegus monogyna* Jacq. with the occasional specimen of *Ilex aquifolium* L. In the grassland, the following species were recorded in 1986: *Anthriscus sylvestris* (L.) Hoffm., *Anthoxanthum odoratum* L., *Taraxacum officinale* Weber agg., *Ranunculus repens* L., *R. acris* L., *Cerastium fontanum* Baumg., *Plantago lanceolata* L., *Trifolium* sp., *Rumex acetosa* L., *R. obtusifolius* L., *Poa pratensis* L., *Festuca pratensis* Huds., *Dactylis glomerata* L., *Holcus lanatus* L. and *Cirsium arvense* (L.) Scop.

The pasture to the west and southwest is grazed by cattle but otherwise unimproved.

The woodland bordering the field to the northwest is known as Colony Reservoir Wood. It is a semi-natural mixed deciduous wood containing 34% *Quercus robur* L. and 57% *Acer pseudoplatanus* L. (figures based on the number of trees and not % cover).

The Marl field (see Fig. 2.1) is grazed by cattle only after August each year in order to conserve some interesting flora. Several plant species occurring in the field were found growing along the northern perimeter of the crop at various times throughout the study. These include *Deschampsia flexuosa* (L.) Trin., *Myosotis discolor* Pers., *Polygala vulgaris* L., *Luzula multiflora* (Retz.) Lej., *Aphanes arvensis* L., *Trifolium dubium* Sibth. and *Holcus mollis* L.

The grazed pasture to the east lies outside the Reserve and is more intensively managed. The fields belong to a different farmer and fertilizers and selective herbicides are applied annually. The fields

are grazed by sheep. Other than the hedge on the southern boundary, dry stone walls separate the arable crop from surrounding fields. These have been in place since their erection during the enclosure period of the late 18th Century (Bullock & Tobin, 1987).

It has been the policy at High Tor Farm to leave a substantial perimeter around the edge of the field unmanaged. According to Mr. Danvers this 'refugium' has remained undisturbed (not ploughed, cut or sprayed) for over 20 years. It is slightly raised above the level of the soil of the field proper and forms a public footpath along the eastern border. It has a total length of 807m and an estimated mean width of $1.97 \pm 0.12\text{m}$ (65 random measurements) and hence an estimated total area of 1590m^2 . This represents 4.6% of the total area of the field bounded by the dry stone walls and hedge.

The hedge and unmanaged boundary together with the central area provide hibernation sites particularly for spring-breeding carabid species which overwinter as adults (Desender 1982). He provides evidence that "the presence of narrow grassland-strips (which are not ploughed or disturbed during winter) in and/or around cultivated fields could ameliorate the refuge and hibernation possibilities for spring breeding carabids and that, as a result of this, in spring much easier colonisation of the fields could occur" (p301). Autumn-breeding species which overwinter as larvae tend to hibernate at depth in the field (Desender, *op. cit.*).

In the centre of the field there is a large rocky outcrop which physically limits access by farm machinery (large rocks which are continually brought to the surface by the plough tend to be discarded here too). Hence another area exists (approximately 40m^2) which is left unmanaged and may also act as a refugium for carabids.

In the three years of the study the field was sown with arable crops. The pattern of crop rotation prior to and during the period of

study was:

Year	Crop
1975-1983	Grassland pasture or hay production
1984	Oats
1985	Spring-sown barley
1986	Oats
1987	Oats undersown with mixed grasses

The crops, once established, were far from being monocultures. Weeds were common and locally abundant in 1985 and 1986. *Fallopia convolvulus* (L.) A. Love, *Polygonum persicaria* L., *P. aviculare* L. and *Stellaria media* (L.) Vill. were the most common.

In 1987, oats were undersown with mixed grasses (the crop was not harvested but used for grazing cattle) and weeds became more abundant later in the year. *Galeopsis tetrahit* L. (sens. lat.), *Holcus lanatus* L., *Anthemis arvensis* L., *Phleum pratense* L. and *Rumex crispus* L. were among the more common species found at various times throughout the year.

Application of fertilizer occurred in 1986 and 1987 only - Fisons granular fertilizer (20:10:10 N:P:K) was applied on each occasion. 2.25 cwt (=33.2kg/ha) was applied to the crop on 30/6/86 (growth stage 2 [Zadoks et al. 1974]) and 2.0cwt (=29.5kg/ha) on 4/4/87 (Growth stage 1). The only other significant organic input was by cattle, which were introduced to the field for short periods only twice during the period of the study: In 1985 on 7th October after harvesting, and in 1987 on 29th August when field work was terminated.

2.2 Carabidae of the arable study site

2.2.1 Initial sampling

Although it is possible to predict which species of Carabidae are likely to be found in a particular habitat (Thiele, 1977), due to the unusual circumstances at Charnwood (the isolation and non-intensive management of the crop) it was decided to determine the faunal composition of the arable field before the main body of research commenced.

Pitfall trap data and pinned collections of Carabidae were available from a variety of habitats at Charnwood from 1974 onwards and this allowed familiarisation with the group in the winter months before sampling commenced. Pitfall traps had been operated in The Marl Field and Colony Reservoir Wood but not in the arable field.

A preliminary investigation into the species composition of this habitat was begun in April 1985 with the placement of 12 pitfall traps at the southern end of the field. This number of traps is more than sufficient to reveal all dominant species in a habitat (Obrtel, 1971). Quadrat sampling and hand collecting were additional methods used to supplement the catch in 1985. The species which were found by a combination of these techniques are listed in Appendix 1. Ten species were chosen for subsequent study and they are presented here in decreasing order of their relative abundance in pitfall traps in 1985. The range of body lengths for each species are those given by Lindroth (1974). Actual measurements of individuals collected from the study site were used wherever possible and these data are presented in the relevant Chapters (see also p.41).

Species	Body Length
<i>Pterostichus melanarius</i> Illiger	12.0 - 18.0mm
<i>Bembidion lampros</i> Herbst	3.0 - 4.0mm
<i>Agonum muelleri</i> Herbst	7.2 - 9.5mm
<i>Bembidion tetracolum</i> Say	4.9 - 6.1mm
<i>Loricera pilicornis</i> Fabricius	6.0 - 8.5mm
<i>Bembidion quadrimaculatum</i> Linnaeus	2.8 - 3.5mm
<i>B.lunulatum</i> Fourcroy	3.6 - 4.1mm
<i>B.guttula</i> Fabricius	2.8 - 3.5mm
<i>Pterostichus niger</i> Schaller	15.0 - 20.5mm
<i>Notiophilus biguttatus</i> Fabricius	5.0 - 6.0mm

2.2.2 General features of species studied at Charnwood

The species listed are all relatively common and widespread in Britain (Luff, 1982b). *Pterostichus melanarius* is mainly a species of open, dry habitats and is commonly found in arable fields (97% of arable fields according to a literature review by Thiele (1977)). It is a medium-sized species and uniformly black with a stout body and long legs. Individuals are "Autumn Breeders" (Larsson, 1939) or larval hibernaters (Lindroth 1949). However, Briggs (1965) found that some individuals bred in more than one season i.e. adults overwintered. *Pterostichus niger* is a typical forest species although it too inhabits arable crops (38% of cereal fields but in 75% of meadows and pastures (Thiele 1977)). It is similar morphologically to *P.melanarius* although individuals are usually larger. Adult beetles are also autumn breeders and again the overwintering stage is larval.

Both species are nocturnal polyphagous predators (Grum, 1966; Thiele & Weber, 1968) and are known to feed on aphids in cereal crops (Vickerman & Sunderland, 1975). Chiverton (1987) collected individuals from the field and examined crop contents - 15.9% of individuals of *P.melanarius* and 55.2% of individuals of *P.niger* contained aphid remains.

Notiophilus biguttatus is a relatively small active species found in a wide range of habitats. The mean body length of individuals collected at Charnwood was 5.00mm which is equal to the lower limit of the range stated by Lindroth (1974). Individuals are diurnally active and a predation strategy is thought to have evolved in this species in which individuals are specialized for feeding on Collembola (Schaller, 1949; Anderson, 1972). Adults breed in the spring and occasionally exhibit a summer diapause. Adults are active well into November at Charnwood.

Loricera pilicornis has a similar pattern of distribution and predatory technique to that of *Notiophilus biguttatus* although individuals can be nocturnally as well as diurnally active (Forsythe, 1987a). Individuals are medium-sized, dark bronze and have distinctive antennae with long stiff lateral setae. The antennae form a "setal trap" (Bauer, 1982) and individuals are specialised for feeding on Collembola (Hintzpeter & Bauer, 1986). The adults are spring breeders having overwintered as adults. Individuals of this species were found in 66% of arable fields in Western Europe (Thiele, 1977).

Agonum muelleri, which is a slightly larger species than *L.pilicornis*, is commonly found in open cultivated habitats. The pronotum is a characteristic vivid green colour and individuals are fast moving. The adult is a polyphagous predator with aphids included in the diet (Vickerman & Sunderland, 1975) and active both by day

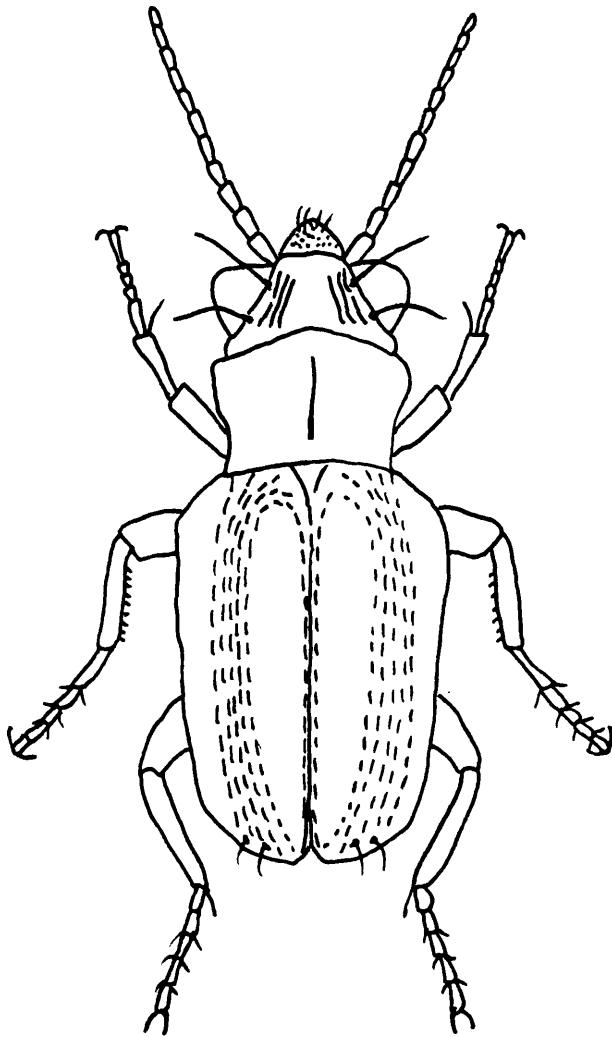


Fig. 2.3 *Notiophilus biguttatus* dorsal view

1.0 mm

and night (own data, Chapter 3). The species is classed as spring breeding with an adult overwintering phase.

Of the five species of *Bembidion*, two are characterized by the presence of two pale spots on each elytron: *B.tetracolum* is nocturnal (Luff, 1978) and is more than twice the size of *B.quadrimaculatum* which is diurnal (own data, Chapter 3). Both are characteristic of open habitats and are commonly found in cereal fields where they have been shown to feed on aphids (Vickerman & Sunderland, 1975).

B.guttula and *B.lunulatum* are superficially similar in appearance but they can be separated on the shape of the basal margin of the pronotum. Both species are black with pale spots at the base of the elytra and are found in open habitats.

B.lampyris is perhaps the most common small carabid in arable crops (found in 86% of arable fields surveyed by Thiele (1977)). It is a small dark bronze species with a shiny pronotum and is aphidophagous (Vickerman & Sunderland, 1975; own observations).

All five *Bembidion* species are classed as spring breeders with overwintering adult phases.

Forsythe (1987b) divides the Carabidae into several subgroups according to external morphology. All species studied here fall into two almost similar structural subgroups with only slight differences in body shape e.g. the slight differences between the prothorax depth:body length ratio (0.19: 0.25 for Carabinae Group I and 0.19 to 0.22 for Carabinae Group II). Evans and Forsythe (1984) and Forsythe (1987b) suggest that the differences in the structure are related to function, with Group I species being generally faster runners. Fast running is sacrificed for more efficient burrowing in Group II species.

N.biguttatus and *L.pilicornis* are placed in Group I along with

other genera of the Carabini: *Carabus*, *Nebria*, *Elaphrus* and *Cicindela*, whilst the other 8 species belong to Group II. However, *N.biguttatus* is a Group I exception in that it has a prothorax width:hind body width ratio more characteristic of the Group II species (0.63 to 0.88:1 as opposed to 0.64 to 0.78:1 for Group I species). Hence 9 out of 10 species studied here all belong to the same structural group, and for the purposes of the present investigation, the slight structural and hence functional differences exhibited by *Loricera pilicornis* are negligible.

2.2.3 Additional material

Additional observations and experiments were carried out on species collected from other habitats (listed in section 2.3.1). In some cases the species were the same as the 10 listed above but additional observations were made on individuals of two other species:

Pterostichus angustatus Duftschmid

Demetrius atricapillus L.

P.angustatus is thought to be nocturnal (Paarmann, 1966). The species is an inhabitant of woodland and forest margins, bare felled patches and burned areas (Thiele, 1977) whereas *D.atricapillus* is commonly found in arable fields (own observations).

2.3 General Methods

2.3.1 Fieldwork

Pitfall trap design

A slight modification to a design already in use at Charnwood Lodge was used in the present study for long-term sampling of Carabidae and in field experiments on avoidance of pitfall traps (see Fig. 2.4).

An outer container (225ml perspex jar: Appendix 2 [i]) with drainage holes in the base accepted an inner container (a plastic drinking cup trimmed down to size: Appendix 2 [ii]) so that the upper rims of the two were juxtaposed. The plastic cup was of such a design as to allow a ridge on its outer surface to prevent it from being pushed into the outer container once the two rims were flush. Being shorter, the inner container was thus secure but suspended within the outer container so that a distance of 4cm existed between the bases of the two.

Drainage holes (diam. = 1.5mm) were made in the sides of the plastic cup using a heated mounted needle. All cups were tested in the laboratory to ensure that the holes were of sufficient diameter to allow the pressure of an almost full cup to exceed the resistance of the surface tension of the water at the holes. Cups could not therefore overflow during periods of rainfall. The drainage holes were large enough to allow small beetles to pass through. Such a passage was possible if beetles remained alive long enough when the level of solution in the cup reached the drainage holes. To account for this, the outer container, into which 'escaping' beetles passed was designed without drainage holes. Beetles could not escape from

the outer container by climbing its sides since the upper rim was in contact with the upper rim of the inner container. When pitfall traps were inspected in the field, the inner container was lifted out and its contents poured into a collecting vessel. The outer container was also searched and, if necessary, extracted from the soil and emptied of water.

The original design of the trap in use at Charnwood until 1984 utilised a metal cover raised above the trap to prevent the entry of water during rainfall and disturbance by mammals and birds. However, preliminary experiments in the field revealed that metal covers placed above the traps selectively captured certain species but repelled others: when covered and uncovered traps were compared it was found that significantly more individuals of 3 nocturnal species and significantly fewer individuals of 4 diurnal species than expected were captured (See Appendix 5). It was therefore decided not to use metal covers but to modify the design of the trap:

- i) To allow rainwater to drain out of the inner container
(see above)
- ii) To prevent predation by mammals (Larochelle, 1975) and birds
(own observations; I. Henderson pers. comm.) by covering each trap with a protective dome of chicken wire secured into the earth with metal pegs (Fig. 2.4).

Preservative solutions are necessary in pitfall traps to prevent desiccation, escape by and predation of captured individuals. There is still some controversy regarding the use of formaldehyde in pitfall traps (Luff, 1968; Adis & Kramer, 1975; Waage, 1985 amongst others) - it may act as an attractant, but unequally at the interspecific level. Its possible carcinogenic properties were also

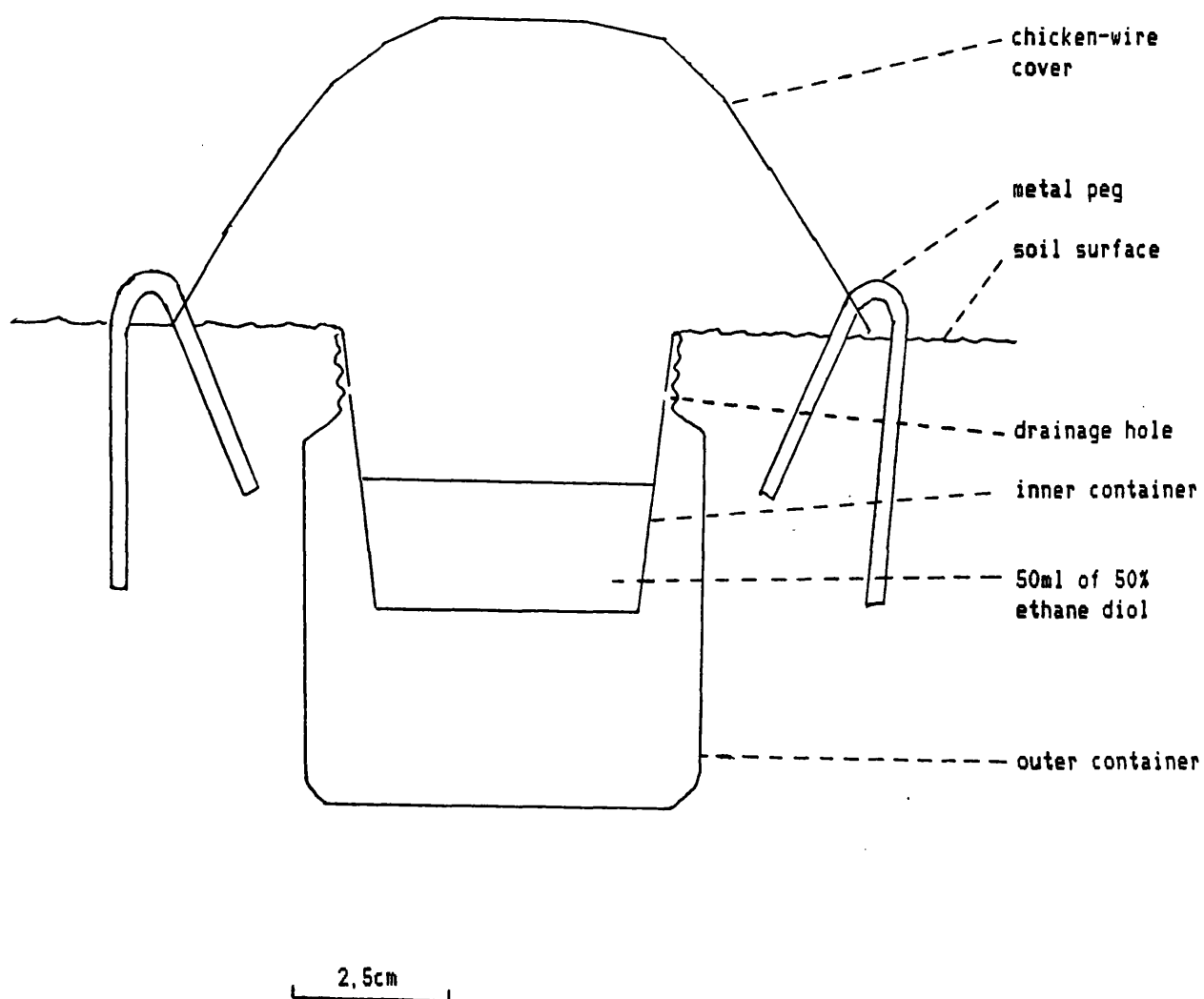


Fig. 2.4 Cross section of pitfall trap in the field.

taken into account and it was decided not to use it in pitfall traps in the present study. Instead, a slight modification to the solution already in use at Charnwood was made. Ethane diol is useful as a preservative (although its preservative qualities are not as great as those of formaldehyde) because it is not volatile and also because it depresses the freezing point of water.

Preliminary observations revealed however, that pure ethane diol has a corrosive effect on some beetles and can react with secretions of mucous from captured molluscs to make separation and subsequent identification of beetles difficult. It was also assumed that very little fieldwork would be carried out when the ambient temperature was below 0°C.

As a consequence, a more dilute solution was used: 50% ethane diol, 20% ethanol and 30% distilled water. The ethanol was added to increase the preservative qualities of the solution. Tests on the solution revealed that

- i) The freezing point was -12°C
- ii) Evaporation of the solution was less than 5% (pbv) in 2 weeks

50 cm³ of this solution was used in each pitfall trap on every occasion i.e. when traps were first placed in the field and on each occasion when traps were emptied of, and replenished with, the preservative solution.

Small pitfall traps were used in the long-term sampling on the Reserve at the southern end of the arable field in 1985, and at the northern end in 1986 and 1987 (see Fig. 2.2). The spacing between the traps, and between rows of traps, was set at 5m.

Year	No. of traps	Dates operated
1985	12	4/6 - 2/12
1986	30	22/4 - 12/9
1987	20	27/4 - 29/7

During certain sections of the study it was necessary to trap a large number of beetles of particular species over a short period of time. It has been shown (Luff, 1975) that the large traps catch relatively large numbers of individuals, especially of larger species. In addition to this though, the number of traps which have to be set into the soil is minimised.

The large pitfall traps used in the present study were plastic containers (Appendix 2 [iii]). These were sunk into the earth and the soil made flush with the upper rim. Chicken-wire covers were used for the same reasons described above. The traps were used for much shorter periods and were inspected more frequently than the smaller traps. Because of this, and due to their greater volume, they were not subject to flooding during periods of rainfall and as a consequence did not have drainage holes.

Large traps were operated in different ways according to experimental requirements. In experiments to determine diel periodicity, a preservative was used in the traps. This was the same solution as was used in small pitfall traps but 200ml was used in each case. For the capture of live specimens, no preservative was used and the traps are referred to as large dry traps.

Physical data

It was not possible to leave recording equipment at the arable study site because of the possibility of interference by humans. The

cottage was therefore used for this purpose. It is located approximately 800m from the arable field and at a similar altitude (see Fig 2.1.) A Grant Squirrel digital meter/logger (Appendix 2 [iv]) was used to record ambient temperature by placing a probe 25cm above ground level in a completely shaded part of the cottage garden so that there was no radiation error. Digital records of the temperature were only taken during pitfall sampling periods. Readings were taken at 15 minute intervals and were accurate to 0.2°C.

An additional maximum-minimum thermometer was used to record ambient temperature in a shaded part of the cottage garden throughout the three years of the study. Readings were taken every 7 days.

Mercury thermometers were occasionally used in the field to check digital records of temperature and to make more frequent records during observations on locomotor activity (Chapter 5).

Rainfall was monitored on the roof of the Cottage using a Cassella rainmeter (Appendix 2 [v]). The rainmeter was capable of continuous monitoring for up to 14 days but was usually emptied of rain water and reloaded with graph paper each week. After heavy rainfall it was often necessary to remove pitfall trap bases to discard collected rainwater. Additional items of equipment were required for this purpose and had to be transported to the study site. Using the rainmeter data collected over the previous week it was possible to determine whether such equipment would be required.

Collection of living material.

Live beetles were collected in three ways: by hand, with the use of a pooter and by using large dry pitfall traps. Beetles were returned to the laboratory the same day or, during protracted periods of study at Charnwood, kept in the Cottage garden. Beetles were

isolated according to body length in plastic petri dishes containing moist filter paper or in aquaria containing moistened substrate from the arable field (see 'Maintenance of cultures' p.40).

Other habitats

Additional observations, collections and experiments were carried out in several other arable fields and in some woodland habitats. Those referred to in the text are referenced below.

Table 2.1

Location	Grid reference	Vegetation type	Dates
Tadcaster N. Yorks.	SE 475 428	Oil Seed Rape	6/86
Billesdon, Leics.	SK 049 718	Winter wheat	5/86
Charnwood	SK 464 159	Winter wheat	1986-87
Charnwood	SK 468 147	Conifer plantation	1985
Llysdimam, Radnorshire	SO 009 585	Deciduous woodland	6/86

2.3.2. Laboratory experiments

Design of pitfall traps for laboratory experiments

Apparatus for studying beetle behaviour with respect to pitfall traps was designed and constructed in 1985. Small pitfall traps, identical to those used in the field, were used in laboratory experiments. The construction of the laboratory apparatus is described in Chapter 4.

Maintenance of cultures

A small (4m x 4m x 3m high) constant temperature room was used at the University for all laboratory experiments and maintenance of living material. The room was illuminated by two 65 watt fluorescent tubes during simulated daylight, and by one infra-red light (Appendix 2 [vi]). A timing mechanism was employed to ensure that the fluorescent lights illuminated the room only during the simulated day. The infra-red light remained on continuously.

Accurate thermostatic control of the temperature was limited by the sophistication of the equipment and so the room could not be maintained at a constant 18 C. However, graphical records of the temperature reveal that the limits were within ± 1.5 C of the intended mean. The humidity of the constant temperature room was not monitored.

Species characterized by small to medium-sized individuals (all species other than *Pterostichus*) were kept in plastic petri dishes (diam. = 7cm) on moist filter paper according to species. Larger individuals i.e. the two species of *Pterostichus*, were maintained in aquaria (1m x 0.5m x 0.5m) containing earth, stones and plants from the habitat from which they were collected. Individuals of *Pterostichus melanarius* and *P. niger* were kept together at a maximum density of 50 individuals m^{-2} . Beetles were fed either crab paste (Sharwoods) or *Xenopus* pellets (*Xenopus* Ltd.) *ad lib*.

More specific details relating to the use of beetles in experiments are given in Chapter 4. Beetles which were still alive after experiments were returned to the habitat from which they came.

Identification, sex and dimensions of beetles

Beetles were identified using the key of Lindroth (1974) and with the aid of specimens in the laboratory. Confirmation of identifications was occasionally necessary and Derek Lott (Leicester Museum), Martin Luff (University of Newcastle), Don Goddard (Coleopterist's Society) and John Bullock assisted in this respect. Nomenclature is according to Kloet and Hincks (1977).

All identification carried out in the laboratory utilised a Kiowa stereo zoom microscope with a magnification range of 7 to 90 times the object. Additional illumination of the object was often necessary and was provided by a Watson light control unit.

Beetles were sexed by dissecting the ventral abdominal sternites (cf. Walsh & Dibb, 1974). With practice, the aedeagus becomes readily visible in males. Occasionally, eversion of the genitalia in dead specimens made dissection inessential.

Physical dimensions of individuals were measured using a Kiowa stereo microscope in conjunction with an Olympus eye-piece micrometer with adjustable guiding needles. Calibration at a variety of magnifications was achieved using a Watson stage micrometer. This system was used to measure body length (defined as the linear distance between the apex of the elytra and the tip of the mandibles in the dorsal view); length of the antennae (the linear distance between the point at which the basal segment is attached to the head and the tip of the apical segment) and maximum diameter of the eyes. Beetles were relaxed and flattened in glycerol for several hours before measurements were taken.

2.3.3. Manipulation and statistical analysis of data

The majority of data were collected manually and transcribed onto the mainframe computer at a later date. Only in Chapter 4 (Experiments 2 & 3) were data entered direct into a computer.

The DEC VAXcluster main-frame computer at Leicester University includes 2 VAX 8600s (48Mb) and a single VAX 11/785 (16Mb). The system supports version 4 of the computer language FORTRAN, the statistical package SPSS (version 8) and the graphical packages GHOST 80 and NAG. FORTRAN was used for data manipulation and simulations and SPSS for statistical analysis of large data sets. All graphs were produced using FORTRAN/GHOST 80 or FORTRAN/NAG programs written by myself, and were printed using a Calcomp 1044 plotter.

In addition to the VAXcluster, a BBC model B micro computer was used to record beetle behaviour in the laboratory and to down-load physical data collected in the field from the Grant Squirrel digital/meter logger. Data were therefore stored on floppy discs but were eventually transferred to the VAXcluster using the KERMIT interactive transfer package.

Further statistical analyses (t-tests and regression) were carried out on a 380Z (Research Machines) computer and an Amstrad PCW8256 microcomputer using software written by John Bullock and myself. All statistical equations were taken from Parker (1979); Kershaw & Looney (1985) and Sprinthall (1987). Paired t-tests were carried out according to the rule of sample size stated by Parker (op. cit.). Data are analysed differently according to the combined sample-size threshold (see Appendix 7).

CHAPTER 3

Periodicity and Abundance

3.1 Diel Periodicity

3.1.1 Introduction

The diel activity patterns (diel periodicity) of carabid beetles have been studied, using a variety of methods, by Drift (1951), Brehm & Hempel (1952), Skuhravy (1957a), Williams (1959a; 1959b), Kirchner (1960; 1964), Greenslade (1963; 1965), Lauterbach (1964; 1965), Grüm (1966), Heydemann (1967), Paarmann & Thiele (1968), Thiele & Weber (1968), Novak (1967; 1968; 1970; 1971a; 1972), Vickerman & Sunderland (1975); McClay (1977); Luff (1978), Löser (1980); Dennison & Hodkinson (1983); Erbeling & Paarmann (1985), Desender et al. (1984); Stubbe et al. (1984) and Ottesen (1985).

Analysis of diel periodicity is usually carried out in the field using pitfall traps. Mechanical time-sorting pitfall traps (used by Williams, 1958; Novak, 1971a; 1972; Luff, 1978; Desender et al. 1984) are particularly useful in such studies. Alternatively, regular manual emptying of traps can be used to gather the data with respect to the time of day (Lauterbach, 1964; Grüm, 1966). Throughout any one 24-hour period it may be assumed that the population density of a species remains virtually constant and hence the numbers of individuals captured is a reflection of the degree of locomotor activity at any one time (assuming the avoidance rate remains constant). When a high proportion of individuals are captured in daylight then the species is said to be diurnal, as opposed to

nocturnal.

Individuals of nocturnal species are occasionally captured (and therefore active) during the day. There are several possible explanations for this. Grüm (1966) demonstrated that individuals of species which are naturally nocturnal will become active in the laboratory during daylight if starved. Thiele & Weber (1968) suggested that for nocturnal species a slight amount of diurnal activity can be interpreted as an avoidance response to an unfavourable change in conditions during the daytime. Similarly, diurnal species can be captured during the dark phase.

To a certain extent, both nocturnal and diurnal species may be crepuscular and hence be taken in traps at dusk or at dawn (methods of trapping can be devised to account for this). Alternatively, it may be that some species are not exclusively nocturnal or diurnal: they are normally active, and can therefore be captured, during both periods.

Other methods used to determine patterns of diel periodicity include direct observations in the laboratory (Greenslade, 1961) and indirect observations using event recorders which can be activated by a moving animal (actographs) (Thiele & Weber, 1968; Erbeling & Paarmann, 1985). Other field workers have specifically identified nocturnal periodicity in carabids capable of flight with the aid of light traps (Williams, 1940; Scherf & Drechsel, 1973; Honek & Pulpan, 1983) but no intraspecific comparison can be made between activity in the light and dark using such a method.

Intraspecific differences in diel periodicity

Results of studies from different localities and habitats are not always comparable as there is evidence that diel periodicity can

differ intraspecifically in these respects. The significance of the conclusion reached by Novak (1971a) when discussing his own results that "relative values of daylight activity agree for some species with observations made by other authors, but there are great discrepancies elsewhere" (p. 149) is important in this context.

a) Spatial differences

Some species have diel activity patterns which vary with distribution, both geographical and at the microhabitat level. Such species were termed 'plastic' by Greenslade (1963). Thiele (1977) offers a slightly different definition - plastic species are those with unstable diurnal periodicity either in a temporal or spatial sense. For example Greenslade (1965) and Löser (1980) found *Loricera pilicornis* to be diurnal in a variety of habitats at Silwood Park, Berkshire and in deciduous woodland in West Germany respectively, whereas Kirchner (1960 - cited in Thiele & Weber, 1968) - demonstrated nocturnal periodicity for the same species in the arable ecosystem in West Germany. In addition to this Novak (1972) and Luff (1978) demonstrated plastic periodicity, with a bias towards nocturnal periodicity, for the same species. Thiele & Weber (1968) found *Loricera* to be 91% diurnal in the field but only 14% diurnal in the laboratory.

It is clear from these and other results that diel periodicity can vary intraspecifically with respect to both latitude and habitat.

b) Temporal differences

Novak (1972) demonstrates shifting patterns of diel periodicity with respect to time. Diurnal species become more active at night in

the height of summer and it is suggested that such changes are responses to unfavourable conditions such as increased temperature and low humidity.

Erbeling & Paarmann (1985) demonstrated that temporal, as opposed to spatial, plasticity of diel periodicity in *Thermophilum sexmaculatum* (F.) in the Sahara allows adaptation to seasonal changes in climatic conditions. This is achieved by shifting the main activity phase within the 24-hour period. Despite this, within a single locality it is unusual to find species containing individuals which exhibit both diurnal and nocturnal activity at the same time of year (Desender et al. 1984). Luff (1978) found that only 20% of field species studied could not be classified as either diurnal or nocturnal. Some workers would refer to these 20% of species as plastic.

It seems then that intraspecific differences in patterns of diel periodicity will often occur when studies are carried out in different habitats and in different geographical localities and similarly, at different times of year in the same locality. The term plastic can be used to describe such species but it can also be used, and will be used in this study, to describe species which show no significant bias towards day or night activity within the same locality. Brunsting (1983) suggests a 70% cut-off point whereby species which demonstrate over 70% activity in daylight (as revealed by pitfall-trap capture) are referred to as diurnal. Similarly, where more than 70% of activity occurs at night, species are referred to as nocturnal.

Interspecific differences in diel periodicity

Within the Carabidae several relationships exist at the interspecific level between the structure of individuals and diel periodicity. Ottesen (1985) found that common species which are characterised by relatively large individuals were mainly nocturnal whilst rare species containing relatively small individuals were mainly diurnal. These findings were based on a study of ground beetles at high altitude and it was suggested that the nocturnal periodicity exhibited by relatively large individuals may be an adaptation to the avoidance of both desiccation and predation by birds. Luff (1978) also found a greater tendency towards nocturnal periodicity in relatively large sized arable-field species.

Relationships between annual and diel periodicity have also been demonstrated. Thiele & Weber (1968) found that 90% of autumn-breeding species were nocturnal. Similarly, Greenslade (1965) and Luff (1978) demonstrated that the majority of spring-breeding species were diurnal.

Apart from the few research papers cited above, relatively little has been done in the field on species of arable land. The combined results of work carried out in arable ecosystems are presented in Table 3.1 in which only the 10 species to be studied at Charnwood are listed. Where there are considerable differences in the literature a compromise definition of the periodicity of a species has been attempted. Where species have not been studied in detail, diel periodicities are listed as 'not known'.

Diel periodicity of 'Charnwood' species

Grüm (1966) inspected pitfall traps in a mixed forest (Pino-Quercetum) habitat every 2 hours and confirmed the nocturnal periodicity of *Pterostichus niger* previously reported by Greenslade (1963). Greenslade (op. cit.) also demonstrated the nocturnal periodicity of *P.melanarius* in a variety of habitats and this finding was confirmed by Thiele & Weber (1968) and others. Further work, mainly by Greenslade (1963), Novak (1971a; 1972), Luff (1978) and Desender et al. (1984) has resulted in a fairly comprehensive list of patterns of diel periodicity of species of Carabidae.

Some workers have attempted to quantify the degree of nocturnal or diurnal periodicity. For instance, Thiele & Weber (op. cit.) captured 18.33% of individuals of *P.melanarius* during hours of daylight and 97% of individuals of *B.lampros*. The corresponding figures for these two species from Novak (1967) are 11% (n=680) and 85.6% (n=187). Both workers concluded that the species were predominantly nocturnal and diurnal respectively. The definition as to whether a species is nocturnal or diurnal is arbitrary but Brunsting's (1983) suggestion of 70% seems acceptable.

Care must be exercised however, to take account of the relative length of the sampling periods; traps are usually left open for more hours of light than dark and this ratio should be taken into account when analysing pitfall data in this respect. For instance, Novak (1972) states that *Loricera pilicornis* is a plastic species with a slight bias towards nocturnal periodicity at Olumec but no correction is made for the fact that traps were operative for more hours of light than dark. Calculation of the expected frequency of individuals captured at night might lead to a different conclusion: that significantly more individuals than expected are captured at night.

Sufficient data were not available in the literature to state categorically what the diel periodicity of *Bembidion quadrimaculatum* or *B. lunulatum* actually is. Novak (1971a) captured only 4 individuals of *B. quadrimaculatum* and other than this the species does not seem to have been investigated with respect to diel periodicity. Brunsting (1983) suggests that the species is diurnal but presents no data or reference in support of the statement. There are no published data on diel periodicity in *Bembidion lunulatum*.

It was one of the aims of the present study to determine the diel activity patterns for these species, and other species to be studied at Charnwood whose patterns of diel periodicity may depend on the type of habitat and locality in which they are found before further work on avoidance and locomotor activity could be carried out.

Table 3.1 Diel periodicity of species of Carabidae to be studied at Charnwood, according to the literature.

SPECIES	DIEL PERIODICITY
<i>B.lunulatum</i>	Unknown
<i>B.quadrimaculatum</i>	Unknown
<i>B.lampros</i>	Diurnal (Novak, 1971a)
<i>N.biguttatus</i>	Diurnal (Luff, 1978)
<i>B.guttula</i>	Plastic/diurnal (Luff, 1978)
<i>B.tetracolum</i>	Plastic/nocturnal(Thiele & Weber, 1968) (Luff, 1978)
<i>L.pilicornis</i>	Plastic/nocturnal(Novak. 1972) (Greenslade, 1963) (Luff, 1978)
<i>A.muelleri</i>	Plastic (Novak, 1971a)
<i>P.melanarius</i>	Nocturnal (Greenslade, 1963)
<i>P.niger</i>	Nocturnal (Grüm, 1966)

3.1.2 Material and Methods

Field studies on diel periodicity were carried out at the study site in 1985 and, more systematically, in June 1986 using large pitfall traps (see Chapter 2) in a 2x11 configuration. Spacing between traps and between rows was 2m and traps were protected from large predators such as birds and mammals by the use of chicken-wire covers, and from predation within the trap by use of 200cm³ of 50% (pbv) ethane diol. Traps were inspected and emptied at dawn and dusk each day and any captured beetles returned to the laboratory for identification.

The duration of the study was limited because of the need to inspect traps manually (no time-sorting trap was available). In 1985, the traps were operated for short periods between 8th and 13th August and in 1986 between 12th June and 8th July inclusive. These short periods were all in multiples of 24 hours commencing either at dawn or dusk so that on each occasion the complete cycle of light and dark was sampled. This criterion was only satisfied in 1986 and the data from incomplete cycles in 1985 is not included in the tabulated results. However, many non-quantitative observations were made in 1985 and are of value. Four additional large pitfall traps were operated over a period of 24 hours in a field of oil-seed rape at Tadcaster, North Yorkshire in June 1986 (See Chapter 2, Table 2.1).

The times of dusk and dawn were taken from 'The Times' newspaper and were approximately equivalent to the time at which street lights were turned off and on respectively in Leicester. No trapping took place for 1 hour before and after these times and so any crepuscular activity was not monitored. Because this investigation was carried out

in the summer, traps were operative for a greater period of daylight compared to periods of darkness and this is taken into account in the statistical analysis of the data.

3.1.3 Results

A total of 83.75 hours of light and 29.42 hours of dark were sampled with respect to beetle activity in 1986. A total of 524 beetles (of the 10 species being studied) were captured and identified to the level of species, 443 being taken in daylight and 81 at night. Of the 10 species studied at Charnwood, individuals of 8 species were represented in the catch - no individual of either *Notiophilus biguttatus* or *Pterostichus niger* was taken.

To demonstrate whether a species was diurnal or nocturnal, a Chi squared test was applied to the data (Table 3.2). The null hypothesis was that all species were plastic and were captured at a constant rate throughout each 24-hour period. Because the traps were operative for more hours of daylight, the expected number of individuals captured to satisfy the null hypothesis was calculated according to the ratio of number of hours trapping in daylight to number of hours trapping in darkness. A significant difference between the observed and expected frequency of individuals captured was found for four of the species, namely *Pterostichus melanarius*, *Bembidion lampros*, *B. quadrimaculatum* and *B. lunulatum* and hence in these cases the null hypothesis was rejected. *P. melanarius* was categorised as nocturnal (more individuals than expected captured at night) whereas the three Bembidiini were diurnal. The diel periodicities of *B. quadrimaculatum* and *B. lunulatum* had not been studied in detail before. Both Novak (1971a; 1972) and Luff (1978) caught too few individuals of the former species for statistical analysis.

Table 3.2 Diel periodicity of Charnwood Carabidae according to field experiments

SPECIES	Ncap (light)		Ncap (dark)		Chi Square	p	DP
	Observed	Expected	Observed	Expected			
<i>P. melanarius</i>	9	29.60	31	10.40	55.13	***	N
<i>B. lampros</i>	186	142.82	7	50.18	50.21	***	D
<i>B. quadrimaculatum</i>	145	112.48	7	39.52	36.16	***	D
<i>B. lunulatum</i>	36	28.86	3	10.14	6.79	**	D
<i>B. tetracolum</i>	6	5.92	2	2.08	0.004	NS	ND
<i>L. pilicornis</i>	7	8.14	4	2.86	0.62	NS	ND
<i>A. muelleri</i>	28	32.56	16	11.44	2.46	NS	P
<i>B. guttula</i>	26	27.38	11	9.62	0.27	NS	P

No. hours trapping in light = 83.75

No. hours trapping in dark = 29.42

Ratio hours light:hours dark = 0.74:0.26

Ncap = number of individuals of each species captured

DP=diel periodicity N=nocturnal D=diurnal P=plastic

ND=no decision due to insufficient data

p=probability that individuals are caught in the ratio 0.74:0.26

***=0.001<p<0.01 **=p<0.001 NS=Not significant (p>0.05)

No significant difference was found between observed and expected frequencies for *Agonum muelleri*, *Bembidion guttula*, *B.tetracolum* and *Loricera pilicornis*. The null hypothesis therefore stands and this would imply that all are plastic species but too few individuals of the last two species were captured for any firm conclusions to be drawn about their pattern of diel periodicity from this set of data alone.

Additional non-quantitative observations of individuals of these 4 species under field cage conditions and in the laboratory suggested that they are predominantly diurnal. Beetles were kept in aquaria and in small petri dishes outside the field centre at Charnwood and were illuminated with red light (1% transmission below 620nm). Observations of these beetles were made frequently at night and, relative to observations in daylight, very little locomotor activity was observed.

Most workers have found *Loricera pilicornis* to be plastic, only Brunsting (1983) regards the species as diurnal. Hintzpeter & Bauer (1986) found that individuals can use either chemical or visual stimuli to locate prey and this may explain why they are efficient predators in both high and low levels of illumination. In contrast, *Notiophilus biguttatus*, a species with a similar predation strategy, has been shown to be an inefficient predator at low levels of illumination since the capture of collembolan prey depends almost exclusively on sight (Bauer, 1979). Individuals of *Loricera pilicornis* were also taken in diurnal quadrat sampling (See Section 3.3) and are certainly active by day at Charnwood. 2 individuals of *Loricera pilicornis* were taken in pitfall traps at Tadcaster during hours of daylight and no individuals were captured at night. For the purposes of this study it was necessary to determine whether species were either nocturnal or diurnal because of the need to use

Table 3.3 Diel periodicity of Charnwood Carabidae according to the literature, field experiments and observations

SPECIES	DIEL PERIODICITY
<i>B.lunulatum</i>	Diurnal
<i>B.quadrimaculatum</i>	Diurnal
<i>B.lampros</i>	Diurnal
<i>N.biguttatus</i>	Diurnal
<i>B.guttula</i>	Plastic/diurnal
<i>B.tetracolum</i>	Plastic/diurnal
<i>L.pilicornis</i>	Plastic/diurnal
<i>A.muelleri</i>	Plastic/diurnal
<i>P.melanarius</i>	Nocturnal
<i>P.niger</i>	Nocturnal

individuals in later experiments. It was therefore assumed, for the purposes of experiments described in Chapters 4 and 5, that *Agonum muelleri*, *Bembidion guttula*, *B. tetracolum* and *Loricera pilicornis* were plastic with a diurnal bias and all experiments involving them were to be carried out in daylight or simulated daylight.

No individuals of *Notiophilus biguttatus* or *Pterostichus niger* were captured during the present investigation. Data from the main sampling grid suggest that individuals of the former species are rarely captured in pitfall traps although they are known to be present in the arable field. The abundance peak of *Pterostichus niger* is displaced temporally from that of *P. melanarius* in all habitats at Charnwood where the two species are present (own data) and the present investigation was carried out during a *P. melanarius* peak. *P. niger* is also much less abundant locally and appears rarely in pitfall traps at Charnwood (J.A. Bullock pers. comm.). Evidence from the literature suggests that the species is nocturnal in all habitats (Grüm , 1966; Thiele & Weber, 1968; Thiele, 1977) and individuals were never observed active during daylight hours under field cage conditions at Charnwood.

In addition to this my own observations at the study site would suggest that *Pterostichus niger* is almost exclusively nocturnal. Several individuals of *P. niger* were taken at night during the mark-release-recapture study presented later in this chapter. Individuals of both *Bembidion guttula* and *Agonum muelleri* were frequently observed active in the arable field during the day and although fewer individuals than expected were captured in daylight, the difference between the frequency of individuals captured during the day as opposed to night was not significant in either case.

3.1.4 Discussion

A study of the literature on this aspect of carabid phenology reveals that diel periodicity patterns are not fixed when the distribution of species is studied. Diel periodicity can be determined by the community in which a species exists. Solem & Sendstad (1978) studied *Collembola* in Scandinavia and found different patterns of temporal partitioning of diel periodicity when the same group of species were studied in different communities. A study of the literature mentioned in the introduction reveals similar differences for the Carabidae. For example *Pterostichus melanarius* has been shown to be more diurnal in grassland habitats than in arable fields or woodland (Thiele, 1977).

Having sounded this warning, the results presented here do not conflict with the results of Luff (1978), from Northumberland, and Novak (1971a) from Olumec, Czechoslovakia, to any great extent. Also, species which were not studied by these authors were captured in sufficient numbers to allow a conclusion to be reached with respect to their periodicity at Charnwood in this habitat. The diel periodicity of *B. quadrimaculatum* had not been studied in detail before. Both Novak (1971a; 1972) and Luff (1978) caught too few individuals for statistical analysis. The diel periodicity of *B. lunulatum* had not been studied at all before. These two species were found to be diurnal at Charnwood.

Very few individuals of *Loricera pilicornis* and *Bembidion tetracolum* were captured but both species were studied in detail by Luff (1978). My own observations lead me to disagree with his findings with respect to *B. tetracolum*, although this conclusion stems from empirical non-quantitative observations (p.54). One explanation of the difference might be that Luff's study was carried

out in an experimental strawberry patch on the edge of an arable field in Northumberland and the difference in latitude or even habitat may explain the observed difference with respect to this species.

It is necessary to make decisions based partly on non-quantitative observations because the patterns of diel periodicity presented in Table 3.3 were used to determine the conditions under which individuals were studied in later experiments on avoidance and locomotor activity described in Chapters 4 and 5 respectively. For these experiments it was necessary to decide if a species was either predominantly diurnal or predominantly nocturnal.

Experiments on diel periodicity do not take into account the possibility that beetles may respond to pitfall traps differently under different conditions of illumination. There may be a bias towards trapping at night because beetles are less able to perceive and avoid traps. Such a possibility was originally suggested, but not tested, by Greenslade (1963). Hence results which suggest that species are plastic/diurnal should be accepted with caution (if such a difference does exist). The problem of fluctuating patterns of avoidance will be discussed in more detail in the final chapter.

3.2 Absolute estimates of population density

In order to test the accuracy of the reinterpretation of pitfall-trap catches using data on avoidance and activity, estimates of the population densities of several species were required. If the overall model (p.16) is a realistic one then it follows that the proportion of individuals captured according to the model should reflect the relative abundance of individuals in the field.

It is difficult to determine population parameters of Carabidae accurately and no single method is suitable for all species. The main quantitative techniques for assessing population parameters are outlined in table 3.4.

Methods such as the use of a sticky frame (Shurovenkov, 1977) can, like pitfall traps, only give relative estimates of population density if some other specific characteristics, such as the relative activity rates and differing capacities for escape from traps, of species are taken into account. The use of insecticides and 'trapping out' methods are not desirable in many situations since they can drastically deplete the population one is attempting to study.

Of the two remaining techniques listed in Table 3.4 (p.60), it can be said that both are useful under different circumstances. Mark-release-recapture is particularly suitable for a relatively abundant species, the individuals of which are readily captured.

Quadrat sampling becomes less efficient as the population density decreases but is useful for diurnal, relatively inactive species which are not easily captured. Both methods were employed in the present study, mark-release-recapture for the nocturnal species *Pterostichus melanarius* and quadrat sampling for other diurnal or plastic species.

TABLE 3.4

The main techniques for estimating absolute population density
in the Carabidae.

TECHNIQUE	SOURCE
1. Quadrat and soil excavation	Briggs (1961); Bankowska & Ryszkowski (1975) Dubrovskaya (1970); Basedow (1973) Sunderland & Vickerman (1980) Desender et.al. (1985)
2. Quadrat and insecticide	Lesiewicz et.al. (1983)
3. Sticky frame	Shurovenkov (1977)
4. Exclusion (trapping out)	Kudrin (1971) Baars (1979b) Desender et.al. (1985) Desender & Maelfait (1986)
5. Mark-release-recapture	Drift (1951) Frank (1971b) Ericson (1977) Loreau (1984) Williams & Knisley (1984) Gordon & McKinlay (1986) Heydemann (1962)

3.2.1 Estimation of population density of *Pterostichus melanarius*

On approaching the problem of which technique to use for this species the following factors had to be taken into consideration:

1. Minimum damage to the crop was essential.
2. Adult *P. melanarius* are known to occur at depths of up to 14cm beneath the soil surface (Desender et al., 1985)
3. *P. melanarius* is predominantly nocturnal (Grewenslade, 1963; Novak, 1971a; 1972; Luff, 1978; own data)
4. *P. melanarius* has a low trap avoidance rate (own data, Chapter 4)
5. *P. melanarius* is a relatively highly mobile carabid (own data, Chapter 5)
6. The use of insecticidal ground sprays (Lesiewicz et al., 1983) and the erection of exclusion barriers were not possible under the circumstances.
7. Individuals of *P. melanarius* do not aggregate in dry pitfall traps (some species do, perhaps in response to pheromones secreted by conspecifics which remain alive in dry traps) (Luff, 1986).

These factors suggested that quadrat sampling would have been an unsuitable technique for this species and that the most obvious choice of technique was mark-release-recapture.

Despite the admonitory stance of theoretical workers (Manly, 1973; Roff, 1973; and others), capture-recapture methods have been used extensively for estimating population parameters in animals. For *Pterostichus* species in particular Drift (1951) and Frank (1971b) worked in deciduous woodland where population densities are usually much lower than in arable crops and grassland (Frank, op. cit.; Thiele, 1977).

TABLE 3.5

Estimates of population density of *Pterostichus melanarius*

Habitat/crop	Technique	No.m ⁻²	Source
Oats	Q	0.6	Basedow (1973)
Winter Wheat	Q	0.6-1.6	"
Arable	Q	0.03	Sunderland & Vickerman (1980)
Pasture	E	15.0	Briggs (1965)
Pasture	E	15.0-22.0	Desender et al. (1985)
Grassy polder	MRR	1.5	Heydemann (1962)
Cabbage	MRR	1.4-5.0	Kirchner (1960)
Winter Wheat	MRR	0.73	Ericson (1977)

Q=quadrat

E=exclusion

MRR=Mark-release-recapture

In the arable ecosystem this technique has been used on *P.melanarius* by Kirchner(1960) and Ericson (1977) (see Table 3.5) with estimates of abundance ranging from 0.73 to 5 individuals m^{-2} . Data from quadrat sampling tend to underestimate population density in this species (Desender et al., 1985 - p.61 point 2) and values in the literature range from 0.03 to 1.6 individuals m^{-2} for arable land.

3.2.2 Material and methods

A mark-release-recapture study was initially attempted in 1985 but a low recapture rate precluded statistical analysis of the data. On this occasion small pitfall traps (see Chapter 2) were used and spacing between traps and between rows was set at 5m. In an attempt to improve recapture data during this study in August 1986, larger traps were used (diameter=10cm: Appendix 2 [iii]) to sample the population in a 2x10 configuration with spacing between both rows and traps within rows being set at 2m. The same study site was chosen with the one notable difference being the crop, which in 1986 was oats compared with spring-sown barley in 1985.

The study was designed to coincide with the period of peak activity abundance (as revealed from pitfall traps in the main sampling grid) which in this species occurred in August.

The 'area of influence' of the grid was determined by Ericson's (1977) method, where the hypothetical perimeter is at a distance from the outermost traps which is equal to half the distance between traps i.e. 1m. The grid was positioned at least 25m from the nearest field boundary and traps were covered with chicken wire to prevent predation by birds and small mammals. No form of preservative was used in the traps since it was necessary to re-release captured

individuals. Some carabids are known to aggregate in dry pitfall traps (Luff, 1986) probably in response to sex pheromones produced by trapped females. However, Luff (op. cit.) demonstrated that aggregation does not occur in *P.melanarius* and so the use of dry traps in the present study is justified.

P.melanarius is subject to intraspecific predation under confined conditions (own observations) and to a lesser extent to interspecific predation by the slightly larger *P.niger*. However, individuals are only partly consumed during such interactions and it is usually possible to identify and quantify trap contents even after predation has occurred.

It was assumed that avoidance of, and any ability to escape from, such traps was equally probable in both marked and unmarked individuals.

Lengthy periods of restriction, handling and disturbance of insects tend to be followed by high levels of activity immediately after release (Greenslade, 1964), therefore traps were inspected as soon as possible after dawn and beetles were then marked in the field and immediately released at random throughout the grid. Beetles were therefore released when they were in their least active phase so that any biased effects resulting from marked individuals being differentially active as a result of disorientation were minimised. Only apparently undamaged individuals were released.

Beetles were not sexed but the precaution was taken to check that all individuals included in the data set were of *P.melanarius* and not the superficially similar *P.niger*. (The diagnostic characteristic is setose tarsi in the former [Lindroth, 1974] which can be determined in the field with the use of a x10 hand lens).

The use of 'Airfix' enamel paints and a sharp tungsten needle was a successful method of marking which I had used previously

on adult parasitic wasps (Lewis, 1984) and was employed with ease in the field. The 'mark' consisted of a small spot of paint applied to an elytron. Such marks were day-specific depending on position or colour, or both. The enamel dried within 2 minutes of application and tests under field-cage conditions revealed that the duration of such a mark was at least 2 weeks. The use of bright colours was avoided to minimise the risk of selective predation by birds.

The study was carried out on four consecutive nights (11-14 August) during which there was minimal rainfall (light rain fell only on the fourth night). The activity period was assumed to lie within the range 20.30-04.30 BST, times which approximately corresponded to dusk and dawn respectively at the time of the study. The same approach was adopted by Novak (1972) in his study of diel activity patterns in the Carabidae - beetles captured between dusk and dawn were classified as nocturnal.

The mean ambient temperatures from nine hourly readings throughout each night are given below.

Night	Min °C	Max °C	Mean °C
1	11.0	12.0	11.6
2	12.2	13.6	12.4
3	13.8	15.6	14.5
4	9.6	12.6	10.5

A separate gutter trap was used to supplement the catch and therefore the number of marked animals released. However, this showed signs of human interference on the second day after which only beetles taken from the dry pitfall traps were used.

Several methods exist whereby the population size can be

estimated from recapture data. Deterministic models include those of Jackson (1939); Fisher & Ford (1947) and Bailey (1951), and of the stochastic models, those of Jolly (1965) and Manly and Parr (1968) are most often used.

Jolly's stochastic model was chosen in preference to the others because of its relative accuracy (Begon, 1979) and because it tends to be more realistic than deterministic alternatives. The Fisher-Ford model is only more suitable when recapture data are poor.

The mathematical steps used in estimating the standard errors are complex and are not presented in full but details can be found in Begon (1979) or in the original paper by Jolly (1965).

Explanation of tabular presentation of data

In the following tables the term 'day' is used in preference to 'night' as is conventional when presenting data using Jolly's model. This also simplifies the presentation of the data as long as one realises that in any one row in Table 3.6 column 2 represents the previous night's capture and column 3 represents the immediate release of those captured individuals. So, for example, individuals captured during the nocturnal activity period between days 1 and 2 are shown, in the table, to have been captured on day 2.

Similarly, in Table 3.7, estimates of population density for any one day are calculated using the data collected during the preceding night.

3.2.3 Results

Capture rate

The greatest number of individuals was captured on the third night when the mean temperature was at its highest during the 4 nights of the study and the lowest number of individuals was captured on the fourth night when both the lowest mean and lowest actual temperatures occurred. There is a significant correlation ($r=0.95$, $n=4$) between the number of individuals captured (dependent variable) and the mean ambient temperature for each of the four periods of nocturnal activity. This suggests that, within this range of temperatures, activity of individual *P.melanarius* increases with temperature.

Recapture rate

Of the 229 individuals marked and released, 49 were subsequently recaptured (21.4% recapture rate). However, the study was terminated immediately after the fourth night so the m_4 individuals were only sampled for one night. If only the marked beetles released on days 1 to 3 are considered, the recapture rate rises to 23.8%, which compares favourably with other studies using the same technique (e.g. Ericson (1977) gives values of 18-30% for the proportion of marked individuals captured subsequent to their release [$=y_i/r_i$]) and was considered sufficiently high to estimate population parameters using the model of Jolly (1965)

Estimates of Population Density

Using Jolly's (1965) method, it is possible to obtain estimates of population size from the data for three consecutive days (Table 3.6). However, the third of these

Table 3.6 Mark-release recapture data.

OCCASION	No. CAPTURED (ni)	No. RELEASED	TIME OF RELEASE OF RECAPTURED MARKS				
			1	2	3	4	5
1	—	73*	—	—	—	—	—
2	30	65*	7	—	—	—	—
3	34	34	4	5	—	—	—
4	61	57	8	8	7	—	—
5	28	—	0	1	1	8	—

Occasion	ri	mi	yi	zi
1	73	—	19	—
2	65	7	14	12
3	34	9	8	17
4	57	23	8	2
5	—	10	—	—

ri = no. of marked individuals released on day i

mi = no. of marked individuals captured on day i

yi = total no. of marked individuals with a day i mark which were
caught subsequently

zi = total no. of individuals marked before day i which were
recaptured subsequent to day i

* = includes individuals caught in gutter trap

Table 3.7 Various estimates from mark-release-recapture data.

Occasion (i)	Mi	$\tilde{N}_i$	θ_i	Bi
1	0.00		0.86 ± 0.27	
2	62.71	243.00 ± 106.08	0.67 ± 0.25	120.81 ± 375.20
3	81.25	284.37 ± 121.38	0.35 ± 0.14	-9.51 ± 35.09
4	37.25	90.02 ± 24.65		

Mi = no. of marked individuals in the population on day i

$\tilde{N}_i$ = estimated total number of individuals in the population on day i

θ_i = estimated survival rate from day i to day (i+1)

Bi = estimated number of additions to the population from day i to day (i+1)

Formulae

$$\theta_i = M(i+1) / (M_i - m_i + r_i)$$

$$B_i = \tilde{N}(i+1) - \theta_i \tilde{N}_i$$

$$M_i = m_i + z_i \cdot r_i / y_i$$

$$\tilde{N} = M_i(n_i + 1) / (m_i + 1) = \text{modified Peterson estimate.}$$

estimates differs considerably from the other two and is perhaps unrepresentative. This is supported by the low value of z_4 (the number of individuals marked before day 4 which were captured subsequent to day 4. The ratio of $z_4:y_4$ is much lower than on previous days and so one explanation for the difference might be that individuals released on days 1 and 2 had reached the perimeter of the hypothetical grid and were therefore less likely to encounter traps than the z_4 individuals.

If the assumption is made that the population remains constant throughout the study period then a realistic estimate of population size can be obtained by calculating the weighted mean. Each estimate is weighted according to the inverse of its variance (Bullock, 1969):

$$P = \frac{\sum (\tilde{N}_i \times V_i^{-1})}{\sum V_i^{-1}}$$

where $\tilde{N}_i$ is the i th population estimate with a variance V_i and P is the weighted mean estimate of population size.

Substituting the first two population estimates from table 3 into the equation:

$$P = 260.95$$

i.e. The mean population size of *P.melanarius* between the 11th and 14th August, 1986 was estimated to be 261 individuals.

To determine the 'area of influence' of the grid the criterion used by Ericson (1977) was employed.

The total area of the hypothetical grid was 80m², which gives a weighted mean population density of 3.26 individuals m⁻²

3.2.4 Discussion

The population density of *P.melanarius* in the arable field at Charnwood during its peak (as revealed by long-term pitfall trapping) is higher than many other values given in the literature (although lower than that of Kirchner (1960) at 5 individuals m⁻²). It may be that the species is unusually abundant at this site since the 'activity abundance' from pitfall data alone is much higher, relative to other species, than in other studies. If, using data from the main sampling grid, the number of individuals captured is taken as a proportion of total carabid capture then the value of 41.7% for the relevant period during August (341 individuals of *P.melanarius*, and 476 individuals of all other species combined, were captured) in the present study is much higher than the value given by Pauer (1975) (19.6% in winter wheat) and others working in arable crops. Martius (1986), working in deciduous woodland, gives a relative activity abundance of 3.7% for this species and a correspondingly lower population density estimate (0.22 individuals m⁻².)

In most studies it is usual to find relative activity abundance values of more than 15% for at least one species and where only one species is dominant this value rises above 30% (Thiele, 1977). Unfortunately, corresponding data on population density is rarely presented but it seems reasonable to conclude that the high density of *P.melanarius* in the present study is a real reflection of the unusually high relative activity abundance at the study site as revealed by pitfall traps.

For the population density estimate from the

mark-release-recapture study to be meaningful it must be assumed that capture does not affect an individual's chance of recapture. Singer & Wedlake (1981) have shown that this is not the case in a lepidopteran species but laboratory experiments suggested, at least in *P.melanarius* that such an assumption is justified: individuals did not 'learn' to avoid traps during a series of consecutive encounters (see Chapter 4). If such a pattern is repeated in the field with larger pitfall traps then differential mortality or activity are left as the only sources of error in this respect.

Despite attempts to minimise the potential effects of differential activity rates of marked and unmarked individuals (see Section 3.2.2) there still exists the problem of starvation of confined and subsequently marked and released individuals resulting in a higher activity rate on the following night. Grüm (1971) has demonstrated increased locomotor activity in starved carabids in the field. Even amongst captured individuals, those caught at the beginning of the activity period would potentially go without food for its whole duration whereas those caught towards the end of the period would hardly be affected in terms of increased activity. Although this represents a potential source of bias in the data (resulting in an underestimate of true population density), the fact that a greater proportion of marked beetles remaining in the field were caught on either the second or third night after their initial capture rather than on the night immediately following their release (see Table 3.6) combined with the possibility that other invertebrates falling into the trap are a potential source of food, suggests that this may not be a problem.

The population density estimate is dependent on the area of influence of the grid which in turn cannot easily be determined where the traps are not placed in an enclosed area (immigration and

emigration can occur). Begon (1979) discusses mark-release-recapture but gives no indication as to how such a parameter should be determined. Dub (1971) suggests that data on the activity of the species should be used but this creates inaccuracy if the distance to the perimeter from the outermost traps is greater than the distance between traps. For *P.melanarius* the distance between traps would have to be approximately 10m since individuals are capable of traversing such a distance in half of the sampling time (simulation and extrapolation from own data presented in Chapter 5) but when traps are spaced at such a distance the recapture rate can only be maintained if the number of marked animals released increases exponentially with inter-trap distance. This, I believe, was the problem in the study attempted in 1985. Here the traps were spaced too far apart to be encountered frequently enough, by the 100 marked beetles, to give a satisfactory recapture rate.

The criterion employed by Ericson (1977) was used in the present study (see p.71) and although this allows immigration and emigration to take place (there is no physical boundary) it can be seen from table 3.6 that recapture rates for r1 individuals (marked beetles released on day 1) do not fall off rapidly after the first night's activity: 9.6% and 6.1% of r1 individuals recaptured on occasions 2 and 3 respectively). This is true also for r2, but not r3 individuals. Nevertheless, these data suggest that individuals remained within the hypothetical grid for some time and that emigration of marked individuals was not as high as expected from data on individual activity and simulation studies.

Roff (1973) presents a complex mathematical formula which suggests that Jolly's model is of limited use unless

$$N \pm 2S.E. < N \pm 0.1N$$

is satisfied, but the sampling intensities required to give such an estimated coefficient of variation can rarely be achieved in practice and despite its weaknesses the model is still widely used with confidence limits well above 10%.

Standard errors of the estimates were fairly constant (44.6%, 42.7% and 36.1% for days 2, 3 and 4 respectively) and although somewhat higher than those of Ericson (1977) (17-27%) and other studies using the same model (e.g. Bullock (1969) (17-26%)), it should be noted that when using Jolly's (1965) model there is a positive correlation between estimates of population size and their estimated standard errors. An estimate with a small estimated standard error can arise either because the estimate is genuinely accurate or because it is a gross underestimate. This means that standard error estimates cannot be relied upon to measure sampling error (Manly, 1971), and indeed "many estimates are more accurate than is indicated by their standard error" (Roff, 1973 p.33).

The weighted mean estimate of population density in *P.melanarius* is used in Chapter 6 in simulation experiments and also in inter-specific comparisons of population density using, for other species, quadrat data collected over the same period.

3.2.5 Estimation of population densities of diurnal species

An alternative method for estimating population density is to use quadrats. Basically, this method of sampling involves delimiting a portion of the habitat by randomly placing a quadrat frame of known dimensions on the soil surface. The beetles within the quadrat (the area bounded by the frame) are counted either directly or after subsequent extraction of a soil and litter sample of predetermined volume.

Random placement of quadrat frames on the soil surface and subsequent extraction of soil to a certain depth is a laborious and relatively inefficient method for estimating population density in this family of beetles since they occur at such low densities (Thiele, 1977). If, for example, soil to the depth of 3cm is extracted from each quadrat then in order to obtain a reliable sample of individuals of most species of Carabidae, many kilograms of soil would have to be dealt with. In addition to this, in the present study it was not possible to collect and subsequently extract soil samples from the study site because of the limited availability of equipment and regard, from the point of view of the farmer, for the state of the field. A compromise between ideal and practical objectives had to be reached and so it was decided to use a quadrat/ground search technique.

It could be argued that in certain circumstances the quadrat/ground search technique is superior to one involving extraction since it relies less on the behaviour of the beetles themselves than do dynamic methods such as the use of the Tullgren funnel where interspecific differences in response to the heat and moisture gradients might affect the results.

The quadrat/ground search technique used here involves visual

observation and direct collection of animals from the soil surface. This is a suitable technique only in certain habitats and with certain species, where it can give estimates that approach the measurement of absolute population density (Southwood, 1978). The technique has been used widely ranging from studies on benthic fauna in streams (Macan, 1958) to the determination of population density in mosquitos (Murray, 1963). In relation to beetles of the arable ecosystem, several workers have adopted the technique (Sunderland et al. 1987a and references therein).

However, the efficiency of the quadrat/ground search method might still depend to a certain extent on the ambient temperature, the time spent searching by the investigator, his powers of detection relative to other investigators, the relative conspicuousness of species and the depth to which the soil is searched or plants and stones within the quadrat are disturbed. In the present study allowance was made for the first two factors only. These factors will be discussed in greater detail in Section 3.2.8.

Despite these disadvantages, the quadrat technique (whether combined with soil and litter extraction or not) has been used to estimate absolute population density in the Carabidae by several workers (see Table 3.4 p.60).

The method is most suitable for studying diurnal species and cannot be used to compare populations of diurnal and nocturnal species since it relies on the visual power of the scientist (unless it is combined with a method of soil extraction). The results of Dubrovskaya (1970) suggest that quadrats and a search of the soil surface is the most efficient method for calculating the population density of diurnal Bembidiini.

It is necessary to collect beetles from the soil surface rather

than record their presence because of difficulties encountered in the identification of individuals to the level of species without the aid of a microscope.

If population density is being determined in a fairly uniform habitat such as an arable crop then the proviso of having a fixed time for searching the quadrats is acceptable (when inter-habitat comparisons are being made it is not). In the present study each quadrat was searched for the same amount of time rather than until all beetles had been removed. This time was long enough in the majority of cases but a correction factor was used to lessen the effect of handling time in quadrats containing many individuals since a certain amount of search time is lost during pooting. The total search time was therefore the sum of the search time (a constant) and the handling time (a variable).

The choice of the size of quadrat depends on several factors, including the population density, motility, and ease of detection and capture, of individuals. For example, when small abundant insects are being studied, it is desirable that the sampling unit should be as small as possible (Southwood, 1978). This is to minimise the chance of some individuals going undetected because they are able to escape whilst the area delimited by the quadrat is being studied.

3.2.6 Material and methods

Investigations took place within the arable field adjacent to the main pitfall-sampling grid. A grid (see Chapter 2, Fig. 2.2) (50m x 20m) was marked out on the soil surface using numbered plastic sticks so that quadrat frames could be placed on it at random. Some preliminary work was carried out in 1985, but the majority of the

data was collected in June and August, 1986 and in May and June, 1987. Samples were taken over short periods which related to periods when carabids were taken in the main pitfall sampling grid. This was so that the two sets of data could be compared.

Preliminary observations and experiments in 1985 were used to determine the optimum size of quadrat to be searched. Sunderland (1975) used quadrat frames which delimited an area of 0.1m^2 but in my preliminary trials a quadrat frame of sides $25\text{cm} \times 25\text{cm}$ (quadrat area = 0.0625 m^2) proved to be the most suitable size (frames delimiting areas of 0.1m^2 and 0.5m^2 were also tested but these areas proved too large to successfully capture all beetles).

In order to sample 0.0625m^2 of habitat, each quadrat frame was placed on the grid according to previously-generated random numbers and then immediately searched for 60 seconds, unless beetles were captured in which case the search time was extended (see below). The efficiency of the method was evaluated with respect to the search time in 1985 and before the method was used to collect the majority of the data. The results of this evaluation are presented in section 3.2.7.

Once data had been collected the results were analysed to determine whether the efficiency of the technique was governed by the ambient temperature which could potentially affect the locomotor activity of beetles and hence their chance of being detected.

Constant reference to a timing device (and potential visual distraction) was avoided by having an electronic stop-watch hanging around my neck which emitted a sound at 60-second intervals signalling the culmination of the search time for one quadrat.

The quadrat was initially searched by visually scanning the soil surface, beginning with the area just inside the edges of the quadrat frame and working inwards. Small stones and recumbent vegetation were

then disturbed and finally the soil was searched to a depth of approximately 3cm using the fingers. Beetles from each quadrat were collected using a pooter and transferred to labelled tubes for subsequent identification. Beetles which could be identified alive were eventually returned to the field.

Each quadrat was searched for an extra period of 5 seconds for every individual discovered within it. This addition to the search time, it was calculated, was the approximate 'handling time' involved in capturing a detected beetle. A second stop watch was used for extending the total time by 5 second units of handling time. It was set to emit a noise every 5 seconds and was activated when the first watch signalled the termination of the search time i.e. 60 seconds.

No allowance was made for varying numbers of stones or recumbent vegetation which were encountered within quadrats nor was the density of erect stems of crop plants (oats or spring barley) since they were assumed to be random within the sampling grid in 1985 and 1986.

3.2.7 Results

The area of quadrat chosen was such that not more than one or two individual carabids were found in a single quadrat. The majority of quadrats contained no individuals. No individuals were observed escaping from a quadrat without being subsequently captured.

An evaluation of the efficiency of the technique with respect to the chosen search time was carried out in 1985. 32 quadrats were searched for a total of 120 seconds in this case and the individuals captured in the first 60 seconds separated from those taken between 61 and 120 seconds. The results reveal that only 1 individual (2%) was found in the latter half of the searching period, in other words the probability of capturing all the beetles of these species in any

one quadrat searched for 60 seconds was 0.98.

On two separate occasions sufficient data were collected within the space of a few days to allow me to investigate the hypothesis that the efficiency of the quadrat method employed (i.e. the proportion of individuals extracted) was proportional to the ambient temperature: the reasoning was that beetles might be more active at higher temperatures and that I would be more likely to see them as a consequence of this. Between the 11th and 12th of June, 1986, quadrats were searched at temperatures ranging from 17.5 to 19.0 °C. When population density is regressed on temperature (the independent variable) then no significant correlation is obtained ($r=-0.0357$, $n=8$). Similarly, between 12th and 15th of August, 1987, beetles were collected at ambient temperatures ranging from 18.0 to 21.0 °C. Once again, no significant relationship between the variables was obtained ($r=0.4226$, $n=6$). Within the very narrow range of temperatures studied here the effect of temperature may be disregarded. In addition to this, a relationship might exist but could be masked by the fact that beetles are not more readily detected at higher activity rates.

A total of 358 quadrats was searched in 1986; 128 between 11 and 12 of June and a further 230 between 7 and 28 of August. 206 carabids of 6 different species were captured (Table 3.10) (individuals of other species were encountered and collected but are not recorded here). The total area sampled was therefore 22.37m². In 1987 a further 864 quadrats (624 in May and 240 in June), representing 54m² were sampled.

The most abundant species was *Bembidion quadrimaculatum* in August 1986 when a mean abundance of 5.75 individuals m⁻² was recorded. However, in June this species was less abundant than *B. lampros* (0.62 and 1.12 individuals m⁻² respectively).

Although no record was taken, it seemed that more individuals were captured in quadrats containing a relatively large proportion of small stones and prostrate species of plants. However, patterns of distribution were found to be random during several quadrat sampling sessions in 1985 and 1986 (Table 3.8). The goodness of fit of the data to the Poisson distribution was tested using the index of dispersion (coefficient of variation) (Southwood, 1978). If the dispersion follows a Poisson distribution then the variance and the mean should be equal. When the variance is less than the mean the population is even more regularly distributed than when described using the Poisson series and when, as is more usually the case, it is greater than the mean the population is more aggregated. The difference between unity and the coefficient of variation is therefore a measure of the departure of the distribution from randomness and this difference can be equated to the student's t statistic as follows:

$$t = (\{s^2/x\} - 1)/SEv \quad (\text{Kershaw \& Looney, 1985})$$

where s^2/x is the coefficient of variation and SEv the standard error of that coefficient. The standard error is independent of both the variance and the mean and is calculated as follows:

$$SEv = (2/(N-1))^{1/2} \quad (\text{Kershaw \& Looney, 1985})$$

The data in table 3.8 clearly support the null hypothesis (that the population is randomly distributed) for all species and for all dates on which samples were taken. *Bembidion lampros* had high positive t values and tended towards a contagious distribution but it may be concluded that the distribution of the population is random

for such a difference could arise by chance quite frequently.

Two factors should be noted with regard to the statistical analysis of this particular data set:

1. The number of individuals captured on each sampling occasion is small.
2. It is a feature of contagiously-distributed populations that the coefficient of variation is influenced by the size of the sampling unit since the mean depends on this (Reise & Weidemann, 1975). On all occasions the mean number of individuals per quadrat was less than unity and thus the chance of detecting slight contagion was reduced.

Pitfall trap captures from the main sampling grid provide an alternative set of data which can be analysed statistically to determine distribution patterns of species. It must be assumed that the probability of each trap being encountered by beetles is equal (i.e. all traps are equally efficient {Greenslade, 1963}). This seems a valid assumption in a relatively uniform habitat such as an arable crop. Tests indicated the data to be randomly distributed (Table 3.9) but in 5 cases species of *Bembidion* showed a contagious distribution. In calculating the number of individuals per trap, only data from traps which were operated for the full duration were used (i.e. traps which were not disturbed and the perimeters of which remained flush with the soil surface).

Isolating individuals to quadrat-specific tubes would have been too time consuming for a study of limited duration and so once the random distribution patterns of species had been established it was decided that all individuals captured in 16 consecutive quadrats

Table 3.8 Distribution of Carabidae: Quadrat data 1985-1986

Species	Date	No. Quads.	Ncap	No./m ²	No./quadrat	s ²	SEv	t	p
B. quadrimac.	110686	128	5	0.63 + 0.28	0.0391 + 0.0172	0.0378	0.1255	0.2528	N.S.
B. lampros	111085	100	16	3.20 + 0.79	0.2000 + 0.0492	0.2424	0.1421	1.4919	N.S.
B. lampros	280985	48	12	5.00 + 1.48	0.3125 + 0.0925	0.4109	0.2063	1.5263	N.S.
B. guttula	110686	128	6	0.75 + 0.30	0.0469 + 0.0187	0.0450	0.1255	0.3328	N.S.
B. guttula	111085	100	2	0.32 + 0.23	0.0200 + 0.0141	0.0198	0.1421	0.0704	N.S.
B. lunulatum	110686	128	9	1.12 + 0.36	0.0703 + 0.0227	0.0659	0.1255	0.5004	N.S.
B. tetracolum	111085	100	4	0.64 + 0.32	0.0400 + 0.0197	0.0388	0.1421	0.2111	N.S.
N. biguttatus	110686	128	4	0.50 + 0.25	0.0313 + 0.0154	0.0305	0.1255	0.2008	N.S.
N. biguttatus	111085	100	9	1.76 + 0.60	0.1100 + 0.0373	0.1393	0.1421	1.8747	N.S.
N. biguttatus	280985	48	10	3.33 + 0.95	0.2083 + 0.0592	0.1684	0.2063	0.9287	N.S.

s² = variance

SEv = standard error of coefficient of variation

t = {(s²/x̄) - 1} * 1/SEv

p = probability that population is contagiously distributed at n-1 d.f. (N.S.=p>0.05)

Table 3.9 Distribution of Carabidae: Pitfall data 1987.

Species	Date	No. Traps.	Ncap	No./trap	s ²	SEv	t	p
B. guttula	May 87	17	57	3.36 ± 0.52	4.7426	0.3536	1.1722	NS
B. guttula	June 87	19	33	1.74 ± 0.25	1.2046	0.3333	0.9193	NS
B. lampros	May 87	17	192	12.00 ± 0.83	10.6276	0.3536	0.3234	NS
B. lampros	June 87	19	309	16.26 ± 1.76	58.87	0.3333	7.8076	***
B. lunulatum	May 87	17	22	1.29 ± 0.29	1.4706	0.3536	0.3856	NS
B. lunulatum	June 87	19	43	2.26 ± 0.51	4.98	0.3333	3.6100	**
B. quadrimaculatum	May 87	17	204	11.29 ± 1.18	23.8456	0.3536	3.1400	**
B. quadrimaculatum	June 87	19	194	10.21 ± 1.18	26.51	0.3333	4.7891	***
B. tetracolum	May 87	17	21	1.24 ± 0.37	2.3162	0.3536	2.4746	*
B. tetracolum	June 87	19	74	3.89 ± 0.55	5.77	0.3333	1.4416	NS
N. biguttatus	May 87	17	16	0.94 ± 0.25	1.0588	0.3536	0.3535	NS
N. biguttatus	June 87	19	9	0.47 ± 1.18	0.49	0.3333	0.0700	NS
P. melanarius	June 87	19	16	0.84 ± 0.27	1.36	0.3333	1.8500	NS
A. muelleri	May 87	17	5	0.29 ± 0.17	0.4706	0.3536	1.6968	NS
A. muelleri	June 87	19	14	0.74 ± 0.20	0.7602	0.3333	0.0820	NS
L. pilicornis	May 87	17	3	0.18 ± 0.13	0.2794	0.3536	1.6497	NS
L. pilicornis	June 87	19	4	0.21 ± 0.10	0.18	0.3333	0.5000	NS

s² = variance t = {(s²/x̄) - 1} * 1/SEv

SEv = standard error of coefficient of variation

p = probability that population is contagiously distributed at n-1 d.f.

*=0.01<p<0.05 **=0.001<p<0.01 ***=p<0.001

Table 3.10 Absolute population density estimates from quadrat data

SPECIES	Ncap	No./m ²	
<i>B.guttula</i>	7	0.87	128 quadrats June 86
<i>B.lampros</i>	9	1.12	
<i>B.quadrimaculatum</i>	5	0.62	
<i>B.lunulatum</i>	1	0.12	
<i>B.tetracolum</i>	0	0.00	
<i>N.biguttatus</i>	4	0.50	
<i>B.guttula</i>	33	2.76	230 quadrats Aug 86
<i>B.lampros</i>	45	3.80	
<i>B.quadrimaculatum</i>	69	5.75	
<i>B.lunulatum</i>	24	1.23	
<i>B.tetracolum</i>	19	1.58	
<i>N.biguttatus</i>	15	1.26	
<i>B.guttula</i>	7	0.18	624 quadrats May 87
<i>B.lampros</i>	46	1.18	
<i>B.quadrimaculatum</i>	36	0.92	
<i>B.lunulatum</i>	5	0.13	
<i>B.tetracolum</i>	1	0.03	
<i>N.biguttatus</i>	3	0.08	
<i>B.guttula</i>	6	0.40	240 quadrats June 87
<i>B.lampros</i>	12	0.80	
<i>B.quadrimaculatum</i>	19	1.27	
<i>B.lunulatum</i>	1	0.07	
<i>B.tetracolum</i>	1	0.07	
<i>N.biguttatus</i>	2	0.13	

(=1m²) would be transferred to one labelled tube. It is not possible therefore to quote standard errors or to determine the type of distribution for the remainder of the data collected in 1986 and 1987. A basic assumption with regard to the quadrat data presented in Table 3.10 must therefore be that all species were randomly distributed within the arable crop.

3.2.8 Discussion

Hughes (1977) found a relationship between activity of bush flies and temperature and corrected his visual estimates of abundance accordingly. It is known that activity increases with temperature in many insect species (Southwood, 1978). A strategy to overcome this when investigating population density is to sample only within a fixed temperature range. This was attempted in the present study but a record of ambient temperature was also made in case a similar correction factor had to be employed. Even so, no relationship was found between ambient temperature and the number of individual beetles captured at an assumed constant population density suggesting either that temperature (within the limited range studied) does not affect locomotor activity, or that it does but any increase in beetle activity does not increase the chance of a beetle being detected by myself in a quadrat.

Whether certain species are more readily detected because of their visual appearance still remains open to question with respect to the present study since no independent evaluation was undertaken (extraction of soil samples was not possible). Species such as *B.quadrimaculatum*, which has two bright spots on each elytron, or *N.biguttatus*, individuals of which have a shiny bronze integument

which reflects direct sunlight, might be more readily detected as a consequence of their increased relative visibility to humans. It is also possible that relatively large beetles are more readily detected, but with the exception of *Bembidion tetracolum*, interspecific differences in mean individual body length in the present investigation were minimal (all species were within the range 3-6mm).

The efficiency of the technique of quadrat sampling employed in this investigation was also evaluated with respect to search time. 98% of carabids were captured in the first 60 seconds when 32 quadrats were searched for 2 minutes and it is concluded that the level of efficiency is acceptable. Brenoe (1987) advocates the use of a soil-soaking technique. After a quadrat sample had been taken this brought any remaining individuals of *Bembidion lampros* to the surface and subsequent extraction of the soil proved the method to be 100% successful. Such a technique might be useful where the soil surface is particularly hard and cannot be disturbed easily but this was not experienced at Charnwood.

The sampling technique might have been biased in that quadrats containing proportionally more prostrate plants and stones (and possibly carabids) were not searched for longer periods.

Both quadrat and pitfall data were used to determine patterns of distribution of species within the arable crop. Estimates of population density from quadrat data in the literature do not normally state the distribution patterns of species - it is simply the number of individuals m^{-2} which is given. In the majority of cases in the present study, species were found to be randomly distributed but species of *Bembidion* were found to be contagiously distributed on 5 occasions. Despite this the decision was made to use the quadrat data collected to determine absolute population density.

Mean values for population densities are presented for six species on several separate occasions and in this respect 2 assumptions must remain:

1. That these are absolute values.
2. That the population of each species was randomly distributed.

Mean values of total carabid population density are frequently quoted in the literature. Frank (1971b) estimated 80 carabids (all species combined) per square meter of arable land in Alberta, and Dubrovskaya (1970) presented mean population estimates ranging from 8 to 51 individuals m^{-2} for Carabidae in arable crops in the USSR.

It is not possible to compare these findings with those of the present study since not all species of Carabidae were collected from quadrats at Charnwood. However, the highest mean number of individuals at Charnwood, when all 6 species are combined, was 16.38 m^{-2} in August 1986. The number of species in the arable crop at the time of the study (from pitfall data) was in excess of 25. Unfortunately, extrapolation is not possible since the relative abundance of all the species in quadrats is not known.

Several estimates of abundance of single species are given in the literature. Sunderland & Vickerman (1980) used the quadrat/ground search technique described here and found a mean abundance of 1.23 individuals of *Bembidion lampros* m^{-2} and 0.67 individuals of *Notiophilus biguttatus* m^{-2} in a variety of arable crops between 1972 and 1977. More specific estimates from the same data set can be found in Vickerman & Sunderland (1975) and Sunderland et al. (1987a), the

maximum values for each species are *B.lampros* 8 individuals m^{-2} in spring barley and *N.biguttatus* 6 individuals m^{-2} in wheat. Values for these species from the present study range from 0.8 to 3.8 individuals m^{-2} for *B.lampros* and 0.08 to 1.26 individuals m^{-2} for *N.biguttatus*. If the mean abundance from the four periods in the present study is taken then the results are similar.

Pitfall trapping (using the main sampling grid) was carried out at the same time as the studies described above. The absolute population density estimates presented here, and in section 3.2 for the nocturnal species *P.melanarius*, are used in simulation experiments (Chapter 6) to attempt to find a relationship between 'activity abundance' (pitfall-trap captures) and absolute abundance.

As argued in the introduction, data on pitfall trap avoidance and locomotor activity are required before this can be attempted. These two parameters will be investigated in Chapters 4 and 5.

CHAPTER 4

Avoidance

4.1 Introduction

The behaviour of beetles encountering pitfall traps was studied experimentally in both the laboratory (1985-1987) and in the field (in 1987 only). Studies were initiated in the laboratory due to the relative ease with which detailed analysis of avoidance behaviour could be undertaken. In addition to the straight-forward responses where a beetle is either trapped by, or avoids, a pitfall trap, a more detailed analysis of the behaviour prior to and during an encounter with a trap was required. This involved observing beetles under constant conditions and recording results on a microcomputer, both of which were not conducive to field studies. Finally, video equipment was employed to analyse behaviour of individuals prior to an encounter in the absence of an observer. This was done to discover whether such behaviour determined the outcome of an encounter, and also whether the presence of an observer affected the outcome of such an encounter. Four different experiments were conducted in the laboratory.

The field experiment was conducted to determine the extent to which the results from the laboratory could be applied to pitfall trap catches in the field.

4.2 Analysis of behaviour in the laboratory

Species studied

10 species of Carabidae which were common in the arable site during the period of this study were subjected to various experimental regimes. These were *Pterostichus melanarius*, *P.niger*, *Notiophilus biguttatus*, *Bembidion lampros*, *B.quadrimaculatum*, *B.guttula*, *B.lunulatum*, *B.tetracolum*, *Loricera pilicornis* and *Agonum muelleri*. This choice represents a cross-section of carabid phenology and in particular with respect to body length and diel periodicity.

Individual beetles were collected from the study site by two methods. The main source for material was large plastic pitfall traps and gutter traps (no preservative or bait was used in the traps). Additional material was collected from the soil surface using a conventional pooter. It was occasionally necessary to supplement the catch with individuals collected from a nearby wheat field on the Reserve (see Chapter 2).

Experimental apparatus and conditions

Live material was kept in a constant temperature room at $18.0 \pm 1.6^{\circ}\text{C}$ and a photoperiodic regime within the ranges of 14 - 16hr light, 10 - 8hr dark was simulated using artificial light in the form of two 65 watt fluorescent tubes and infra-red light (1% transmission below 620nm: Appendix 2 [i]) respectively. All experiments were conducted between 1st May and 1st September and the photoperiod adjusted accordingly. The artificially-simulated 24-hour day corresponded as closely as possible to the actual periods of light and dark in the field with respect to the times of dawn and dusk, so

that beetles from the field did not experience a sudden displacement of their internal 'clock' relative to their perceived day.

Pterostichus species were kept in aquaria which contained moist soil from the study site, whereas the other species were kept on moist filter paper in petri dishes (diam. 10cm) at a maximum density of 10 beetles per dish. Species were separated where possible but it was often necessary to mix *Bembidion* species which could not be identified *in vivo*. All beetles were fed commercially-available crab paste or *Xenopus* pellets (*Xenopus* Ltd.) *ad. lib.* and were used in experiments within 7 days of their initial capture.

An artificial arena for studying behaviour was made from two clear plastic sandwich boxes which were glued with their open ends juxtaposed (see Fig. 4.1). The lower of these two boxes had a smooth Plaster of Paris surface flush with its upper rim. Two pitfall trap containers were sunk into the longitudinal axis of this surface before the plaster had set so that the rim of each trap and the plaster formed a continuum. The base of the upper of the two boxes was cut away to allow access to the arena so that beetles could be introduced onto the plaster. This also allowed access to beetles throughout the arena during the course of any experiment. The sides of the upper box thus formed a boundary to the arena. Beetles were unable to climb the smooth plastic 'walls' of the arena and so throughout any experiment they remained within the horizontal plane of the Plaster of Paris surface or within one of the pitfall traps.

The arena was designed with two traps to allow 'choice' experiments to be conducted with respect to the type of solution used in the plastic cups (see experiment 4).

Small traps were used which were of the same design as those used in the field (See Chapter 2) except for the absence of wire covers. 50ml of 50% ethane diol was used in each cup in all four

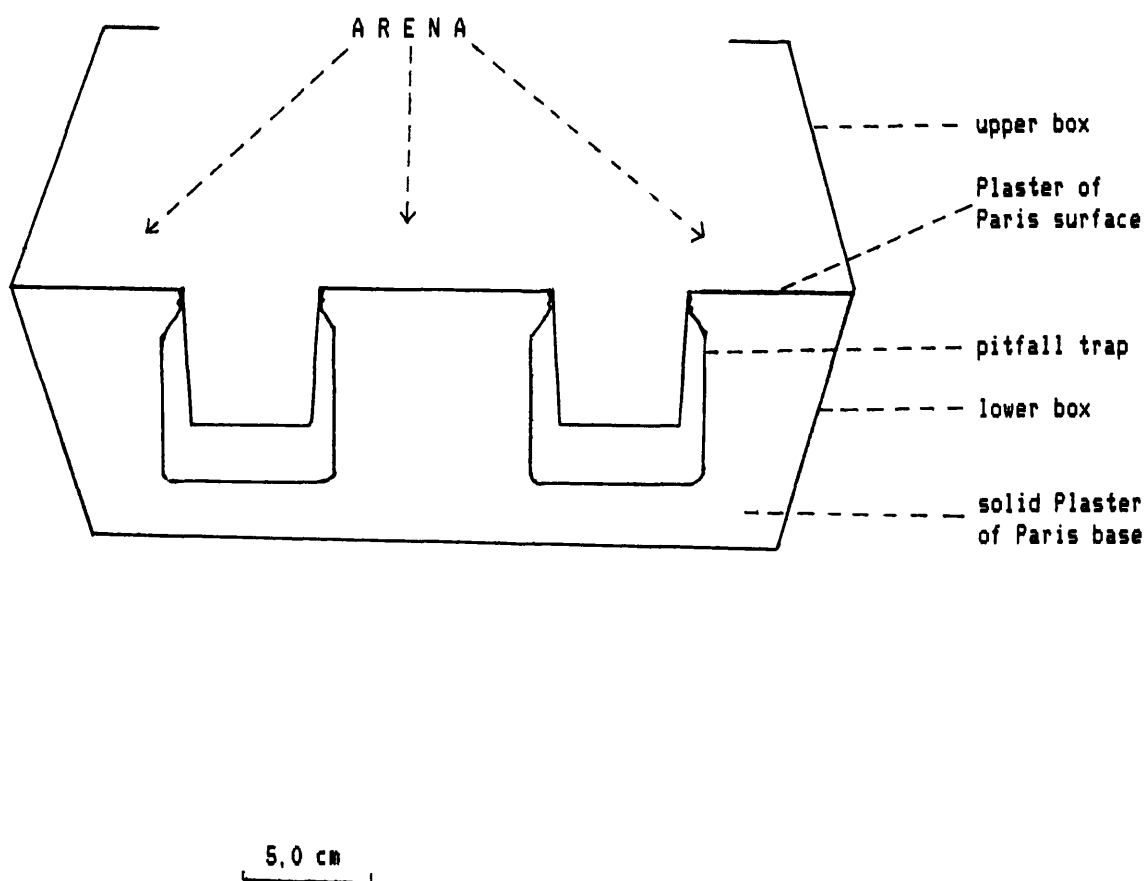


Fig. 4.1 Diagram of cross section along longitudinal axis of laboratory apparatus used for studying avoidance behaviour..

Area of arena = 448 cm²

% of area occupied by traps = 10.61%

experiments.

Experiments conducted using diurnal carabids took place under artificial illumination of the simulated photoperiodic 'day' and nocturnal species were observed under low intensity red light (Appendix 2 [i]) which illuminated the CT room throughout the simulated 'nights'.

Experiments on diurnal species were conducted at any time from 6 hours after the commencement of the artificial day to 4 hours before commencement of the 'night'. Experiments on the two nocturnal species were conducted between 1 hour after 'dusk' and 3 hours before 'dawn'.

Experiments were conducted at different densities of individuals according to species and experimental requirements (see table 4.1). Preliminary observations suggested that 20 individuals of *Notiophilus biguttatus* or 30 individuals of *Bembidion* species were the maximum densities at which direct observation of encounters with pitfall traps could take place. At higher densities, the chance of simultaneous encounters occurring increased, but the recording technique for most of the experiments allowed only one encounter to be recorded at any one time. Generally, beetle activity, and therefore encounter rate, increases with body length (pers. obs.) and so lower densities were chosen for the larger carabids. The lowest maximum experimental density was 8 individuals for both *Pterostichus* species.

TABLE 4.1 - Maximum densities of species in
laboratory experiments.

Species	Max. Density	Expt. in which used
<i>B.guttula</i>	30	1,2
<i>B.quadrimaculatum</i>	30	1,2,4
<i>B.lampros</i>	30	1,2
<i>B.lunulatum</i>	30	1,2
<i>N.biguttatus</i>	20	1,2,3,4
<i>B.tetracolum</i>	20	2
<i>L.pilicornis</i>	15	1,2
<i>A.muelleri</i>	15	1,2
<i>P.melanarius</i>	8	1,2
<i>P.niger</i>	8	1

Because some of the beetles in experiments 1 and 2 had been collected from the field using large dry pitfall traps they had already encountered a trap at least once. It is initially assumed that this did not affect their response on encountering the small traps in the laboratory and in a later analysis of results this is tested.

4.2.1 Experiment 1 - Manual monitoring of behaviour

The following factors were taken into account during the design of the first experiment:

1. Simulation studies (see Chapter 6) using field data on individual activity suggested that beetles will rarely encounter a pitfall trap twice when small traps are spaced at 5m intervals. The mark-release-recapture study on *P.melanarius* (see Chapter 3) was conducted using large pitfalls at a relatively high density and even then the recapture rate was about 10% over a period of 24 hours. As is shown later in the present chapter, this is equivalent to a 13% encounter rate in this species since all individuals which encounter a trap are not captured. In the main sampling grid, traps were smaller and set at a lower density thus reducing even further the possibility of multiple encounters.

2. The possibility that an individual beetle's response at successive encounters may be affected by its initial encounter had to be taken into account. If the beetle is released into the arena again after it has either been trapped or has avoided a trap, any subsequent response could be influenced by the deleterious effects of handling after the initial response, or by the insect becoming 'familiar' with a trap as the number of consecutive encounters increases. In other words, an encounter may affect an individual's behaviour during a subsequent encounter, regardless of the type of response following it.

3. Substantial alteration of trap design would have been necessary if beetles were to fall into the trap but not come into contact with the

toxic solution (even if beetles could be removed from the toxic solution quickly, such contact could still have affected their subsequent behaviour at any further encounter). It was also unclear, during the design stages of this experiment, whether beetles were attracted to ethane diol or not, and an alteration to the design of the traps which reduced the surface area of ethane diol, and hence the detectability of the solution could have affected the applicability of the results to the field situation.

It was therefore decided that the most suitable approach was to test an individual beetle's response once only, and to make the assumption that any individual would avoid the trap with a fixed probability which was species-specific, and that the final ratio of the total number of avoidances to the total number of individuals captured would be equivalent to this probability.

Experiment 1 - Method

The purpose of this experiment was to determine the rate of avoidance of several species of Carabidae by observing beetles encountering small pitfall traps and recording the results manually.

Individuals which were captured by a trap were left in the trap for the duration of the experiment and individuals which avoided were removed from the arena as soon as possible using a pooter or, for the species of *Pterostichus*, by using a pair of forceps, with the minimum possible disturbance to the individuals remaining in the arena. In replicates of this experiment, where individuals of several species of *Bembidion* were present in the arena and the response times of individual beetles was required, individuals were

removed from traps as soon as possible after they were captured using a pair of long forceps, again with minimum disturbance to the other beetles in the arena. These individuals were isolated for subsequent identification.

As each experimental replicate proceeded therefore, the density of individuals, and hence the frequency of encounters, decreased. Replicates of the experiment were terminated after 30 minutes, or sooner if all individuals had encountered and responded to one or other of the traps.

Before the recording of behaviour commenced, beetles were introduced to the arena but denied access to the trap perimeters by placing upturned plastic cups over each trap for a period of 5 minutes in each experiment. This was to allow them to become accustomed to the apparatus and for any initial relatively high activity rate to decrease. The plastic cups were carefully removed immediately before activating the monitoring program.

Experiment 1 - Results

The recording technique proved successful for all species studied. Occasionally more than one encounter occurred simultaneously but it was still possible to record the outcome of each encounter. A total of 465 encounters were recorded in this experiment. The results are summarized in Table 4.2. These represent the first response of each beetle to an encounter with a small pitfall trap and therefore the rate of avoidance of such a trap exhibited by the species.

Individuals of only nine of the ten proposed species were studied in the first experiment. This was because individuals could only be tested according to their availability. The other species,

TABLE 4.2

Avoidance rates for species studied in experiment 1

SPECIES	No. TRAPPED	No. AVOIDED	% AVOIDANCE
<i>B.guttula</i>	2	8	80.00
<i>B.quadrimaculatum</i>	30	62	67.39
<i>B.lampros</i>	32	120	78.95
<i>B.lunulatum</i>	0	4	100.00
<i>N.biguttatus</i>	6	69	92.00
<i>B.tetracolum</i>	1	1	50.00
<i>L.pilicornis</i>	0	0	-
<i>A.muelleri</i>	6	30	83.33
<i>P.melanarius</i>	36	8	18.18
<i>P.niger</i>	43	7	14.00

Loricera pilicornis, was studied along with these species in experiment 2. As a consequence of the low availability of some species in the field, very few individuals of *Bembidion guttula*, *B. lunulatum* and *B. tetracolum* were studied. Hence little significance can be attached to the rates of avoidance for these three species (more individuals were tested in experiment 2).

Agonum muelleri was shown to be a plastic species with respect to diurnal periodicity in chapter 2, in this experiment however, all individuals were tested in artificial daylight. An avoidance rate of 83.33% was found for this species.

The species are listed in Table 4.2 in order of increasing body length - the significance of which will become apparent later. These results will be discussed in greater detail after those of experiment 2 have been presented since the two experiments were identical except for the recording technique employed.

4.2.2 Computer monitoring of behaviour

Whilst replicates of experiment 1 were being carried out, the monitoring program "Beetle" was developed (see below). This was partly in response to difficulties in recording responses on paper but also because a method of analysing responses in more detail, particularly with respect to time, was required.

A BASIC program (See Appendix 3) was written for the BBC computer which allowed several aspects of individual behaviour to be recorded relative to the program's built-in clock. Data were entered via the keypad by pressing the key which corresponded to a particular behavioural change of an individual as it occurred. By this method a screen menu with a constantly updated results section was modified throughout the experiment. A final data file containing a record of

every behavioural change and the time at which it occurred was produced and could be transferred to the mainframe computer for statistical analysis.

The same apparatus was used in the same position in the CT room (see Plate 4.1). The only difference was the proximity of the microcomputer which emitted green light.

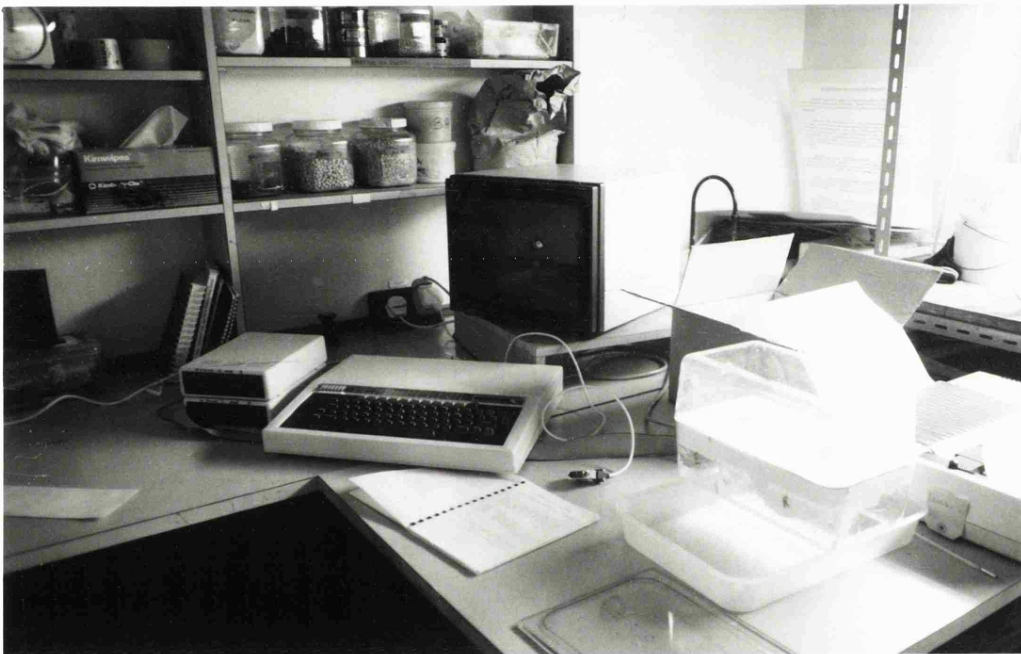


Plate 4.1 Apparatus used in Experiments 2 & 3

For any experimentally observed individual, three aspects of behaviour could be recorded with respect to time, with two additional responses (considered instantaneous for the purposes of the time budget) being recorded at the termination of an encounter.

The three behavioural categories were termed 'stationary', 'walking' (any form of movement of an individual relative to the

arena), and 'encountering', where an encounter involved a physical interaction between a beetle and the perimeter of one of the two traps.

An encounter commenced when the legs or antennae of a beetle made contact with the perimeter of a trap and ended when contact with the trap perimeter ceased either because the insect fell into the trap, or avoided it by moving away. Thus the two possible responses following an encounter were termed 'trapped' and 'avoided'. Beetles could therefore only avoid a trap by entering the behavioural category 'walking'.

These behavioural categories and responses soon become easily recognisable and adjacent letters on the keypad were chosen to correspond to the five possibilities so that as an individual beetle's behaviour altered, the corresponding key could be depressed (the menu actually allows for six possibilities since an encounter with either one of two traps was possible). A seventh key, S, had the function of terminating the experiment by stopping the clock and writing the data file. The final menu is therefore a record of the time spent in each of the three behavioural categories and a summary of the behavioural sequences associated with an encounter. For a more detailed analysis of each encounter it was necessary to work with the complete data file on the mainframe computer.

It was possible, with practice, to record behavioural changes as and when they occurred without removing one's eyes from the arena. The monitor was positioned so that quick reference to the clock and to the number of encounters was possible (the two factors which determined the duration of an experiment).

A behavioural sequence could be recorded, for example, as Q-W-E-T, with a time accurate to one millisecond associated with each change. In this example sequence the insect was initially

stationary (Q), it then walked (W) until it encountered a trap (trap 1), and was subsequently captured by this trap (T). It is therefore possible to extract from the data the time spent encountering the trap, which is given by $t_T - t_E$. A separate key, (R), was used for encounters with trap 2 and the key Y used to indicate avoidance.

In experiment 2 the behaviour of any beetle in the arena which encountered a trap was recorded, and hence for the purposes of data analysis all records of behavioural sequences contained only E,R,T & Y. In these experiments, the key for walking (W) was used between encounters only for the purpose of keeping the clock activated. The full complement of keys (Q,W,E,R,T & Y) was only used when individual beetles were continuously monitored (experiment 3). For a summary of the experiments with respect to the types of behaviour monitored see Table 4.11 (p.136).

4.2.3 Experiment 2 - Method

The purpose of this experiment was to determine the rate of avoidance of the species already studied in experiment 1 more accurately by increasing the number of encounters for each species, but particularly for those species for which no, or very few, encounters had been registered (see Table 4.2 p.99).

Experiment 2 - Results

Avoidance rates

A total of 495 encounters was recorded in this experiment - 480 of these were recorded via the computer. Occasionally, more than one encounter occurred simultaneously, in which case only one encounter

was recorded via the program and the other recorded manually. The further 15 encounters were recorded manually when simultaneous encounters occurred. The responses which were recorded manually could not be analysed with respect to time and are in effect additional data for experiment 1.

Because the clock was momentarily stopped each time a response was recorded, the actual duration of experiments, although not quantified, was slightly longer than the final time displayed on the clock. However, for the purposes of the time budget this is considered to be irrelevant.

The results of the two experiments are combined (Table 4.3) since the only difference between them was the recording technique employed. From the combined results, a high number of replicates was obtained for four species in particular, with over 100 individuals tested in each case. Three of these species were diurnal (*Bembidion lampros*, *B. quadrimaculatum*, and *Notiophilus biguttatus*) and had avoidance rates which were high relative to the nocturnal species *P. melanarius*.

Trap efficiency

When the results from all species are pooled then it can be seen that more encounters took place with one of the two traps (Table 4.4) and that this difference is a significant one (Chi square = 7.01; $0.001 < p < 0.01$).

However, when results were pooled, there was no significant difference between the rates at which beetles were trapped by or avoided the two traps in experiment 1 i.e. both traps were equally efficient.

Avoidance rates and mean body lengths of species studied in experiments 1 and 2.

SPECIES	No. TRAPPED	No. AVOIDED	%AVOIDANCE	$\text{SIN}^{-1} \sqrt{pa}$	BODY LENGTH (mm)	SEy * $t_{p=0.05}$
B.guttula	9	26	74.28	59.53	3.11 ± 0.045 (N=13)	17.10
B.quadrinaculatum	58	99	63.06	52.57	3.32 ± 0.045 (N=21)	16.74
B.lampros	35	138	80.23	63.60	3.67 ± 0.042 (N=27)	16.15
B.lunulatum	8	19	70.37	57.02	3.80 ± 0.065 (N=10)	15.95
N.biguttatus	28	182	86.67	68.56	5.00 ± 0.030 (N=61)	14.32
B.tetracolum	6	12	66.67	54.74	5.16 ± 0.012 (N=10)	14.14
L.pilicornis	39	34	46.57	43.03	7.05 ± 0.084 (N=10)	13.14
A.muelleri	15	65	81.25	63.23	7.36 ± 0.035 (N=10)	13.16
P.melanarius	115	22	16.06	23.62	14.32 ± 0.243 (N=10)	24.23
P.niger	43	7	14.00	21.97	17.52 ± 0.204 (N=10)	32.09

$\text{Sin}^{-1} \sqrt{pa}$ = arc sine of $\sqrt{\% \text{avoidance}/100}$

SEy * $t_{p=0.05}$ = Standard error of $\text{Sin}^{-1} \sqrt{pa}$ * 2.262

FIG. 4.2 RELATIONSHIP BETWEEN
AVOIDANCE RATE AND BODY LENGTH

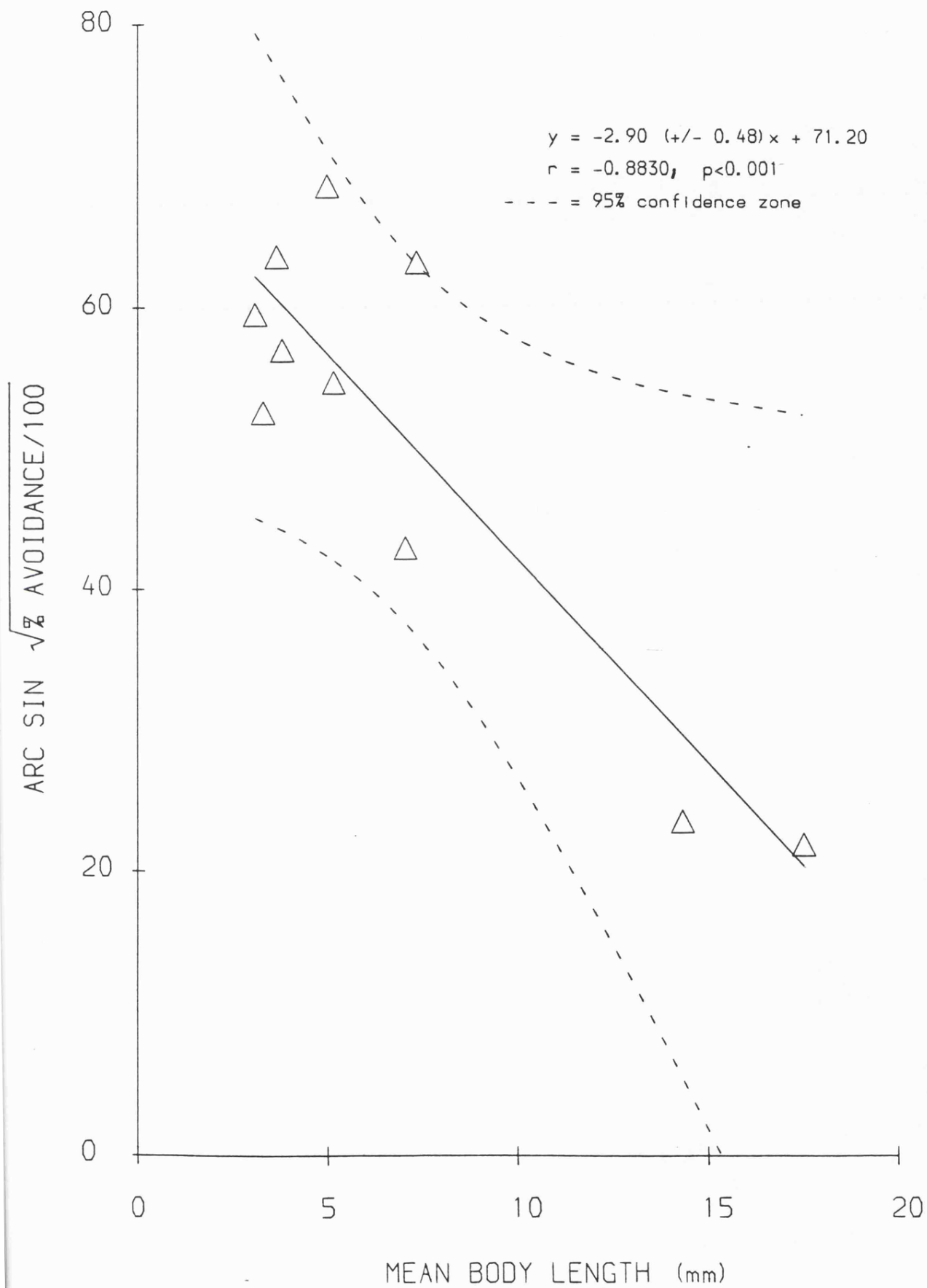


TABLE 4.4

Statistical tests on the experimental apparatus

Trap Encountered	Response	Frequency
Trap 1	Trapped	156 (A)
Trap 2	Trapped	200 (B)
Trap 1	Avoids	266 (C)
Trap 2	Avoids	338 (D)

Encounters Trap1/Encounters Trap 2	Chi square = 14.01 (***)
Trapped by 1/Trapped by 2	Chi square = 0.003 (NS)
Avoids 1/Avoids 2	Chi square = 0.002 (NS)

*** = $p < 0.001$ NS = $p > 0.05$

Expected frequency encountering trap 1 or 2 = $(A+B+C+D)/2$
 Expected frequency trapped by trap 1 = $(A+B)*(A+C)/(A+D+C+D)$
 Expected frequency trapped by trap 2 = $(A+B)*(B+D)/(A+B+C+D)$
 Expected frequency avoiding trap 1 = $(C+D)*(A+C)/(A+B+C+D)$
 Expected frequency avoiding trap 2 = $(C+D)*(B+D)/(A+B+C+D)$

Table 4.5 - Comparison of rate of avoidance of material from different sources

SPECIES	Observed Frequency Encounters (Pooted) A	Observed Frequency Encounters (Trapped) B	Observed Frequency Avoidance (Pooted) C	Observed Frequency Avoidance (Trapped) D	Expected Frequency Avoidance E	Expected Frequency Avoidance F	Chi Square p
B.guttula	26	9	20	6	19.31	6.69	0.0958 N.S.
B.quadrinaculatum	55	102	34	65	34.68	64.32	0.0205 N.S.
B.lampros	30	93	27	82	26.58	82.41	0.0087 N.S.
B.lunulatum	23	4	15	4	16.19	2.81	0.5914 N.S.
B.tetracolum	16	2	11	1	10.67	1.33	0.0921 N.S.
N.biguttatus	182	27	160	22	158.49	23.51	0.1114 N.S.
L.pilicornis	1	72	0	34	0.47	33.53	0.4766 N.S.
A.muelleri	1	57	1	45	0.81	45.21	0.0455 N.S.

Calculation of expected frequencies for chi squared test: $E = (C+D)*A/(A+B)$ $F = (C+D)*B/(A+B)$
 p = probability that avoidance rates are equal for material from the two different sources
(N.S. = $p > 0.05$)

'Learning'

An original assumption was that any difference in the past experience of beetles (with respect to encountering pitfall traps in the field) would have no effect on their behaviour upon encountering a pitfall trap in the laboratory. This assumption was tested by comparing the responses of beetles collected from the field by 2 different methods: by dry pitfall trapping and by pooting. Data presented in table 4.5 show that there is no significant difference between the frequency of avoidance of the 2 groups.

Body length and avoidance rate

A significant relationship exists between avoidance rate and mean body length for the 10 species studied (see Table 4.3; Fig. 4.2). Body length was determined by measuring the distance, in preserved specimens, between the tip of the nasale and the extreme apex of the elytra in dorsal view. For the graphical presentation of the data, the values for the % rate of avoidance have been transformed according to the equation $\sin^{-1} \sqrt{p}$ (where $p = \% \text{ avoidance}/100$). This is because data in the form of percentages tend to be binomially distributed. The arcsine transformation is used since the range of p is greater than 0.5 ± 0.2 (Parker, 1976).

A correlation coefficient (r) of -0.8830 with 8 degrees of freedom was obtained from analysis of the transformed data and this was significant ($p < 0.001$)

The equation which is derived by regression analysis is:

$$\sin^{-1} \sqrt{p} = -2.90 (\pm 0.48) \text{ body size} + 71.20$$

and is statistically significant ($t = B/SE_B = 2.48$ ($0.01 < p < 0.05$ at 8

degrees of freedom)).

The standard error of y for chosen values of x is used to mark out the 95% confidence zone for any estimated value of y using $SE_y * t$ at $p=0.05$ (see Appendix 7).

A more meaningful descriptive statistic is the standard error of estimate (Sprinthall, 1987). This is a general standard error (for all values of y) can be computed using the following formula:

$$SE_{est} = S_y [(1 - r^2) * (N/N-2)]^{1/2}$$

Where S_y = the true standard deviation of the y -sample.

$$= \pm 8.56$$

It can be used to establish the accuracy of any one predicted y -variable. The value will always be between 0 and S_y , and when $r=1$ (a perfect correlation) $SE_{est} = 0$.

An inverse relationship exists between the two variables - as body length increases the rate of avoidance of pitfall traps decreases. This relationship gives support to the hypothesis that avoidance rate is related to the body length of a beetle.

However, the variables are only significantly correlated if the two relatively large *Pterostichus* species are incorporated in the statistical analysis of the data. When only the eight smaller species are considered, the correlation coefficient has a value of -0.2104 ($p>0.05$ at 6 degrees of freedom).

Response time

The response times for individual encounters can be extracted from the data by subtracting the time of an encounter, relative to the internal clock of the program, from the time of the response following it.

For several of the species studied analysis of the data from the time-budgeting program reveals significant differences between the times taken for the two types of response to occur after an individual initially encounters a trap. In encounters where a beetle is subsequently trapped (a type 1 response) then the time spent encountering the trap is significantly shorter than the times recorded for beetles which subsequently avoid a trap (a type 2 response) in the following species: *B.quadrimaculatum*, *B.lampros*, *B.lunulatum*, *N.biguttatus*, *L.pilicornis*, *A.muelleri*, and *P.melanarius*. The other two species studied (*B.guttula* and *B.tetracolum*) show no significant difference in this respect. (see Table 4.6).

One factor which should be taken into consideration is the delay in recording a type 1 response once it has occurred. The time at which such a response occurs cannot be predicted (unlike a type 2 response) - the assumption from the point of view of the time-budgeting program is that a type 2 response occurs once the beetle breaks contact with the trap perimeter and all 6 legs are in contact with the Plaster of Paris surface. This is not an instantaneous process and to a certain extent the observer is ready to register the change in behavioural categories (from Y [avoidance] to W [walking]) as it occurs. The opposite is true of a type 1 response - here the insect does not gradually fall into the trap but the process happens much more quickly and the observer records it after it has happened and without anticipation. To overcome this

problem an independent method of assessing the observer's powers of response to a random event was used. A stop watch was set to emit an audible noise which was random with respect to time (it is recognised that detection of such an event is auditory rather than visual, but equipment which would emit a random visual event could not be obtained). The use of an auditory event can be justified if it is realised that the distance between the object and the ear was such that the sound reached the ear in less than 0.0003 seconds, and for the purposes of detection by the brain this delay, relative to the speed of light, can be considered negligible).

The delay in recording such an event was calculated by subtracting the time at which it occurred from the time at which it was recorded on the computer. The mean time for this delay was 0.220 ± 0.035 seconds ($n=10$).

If this value is subtracted from each type 1 response time then the difference between the mean times for the two types of responses is increased without affecting the standard error for the 8 species mentioned above. However there is still no significant difference between the mean response times for *B.guttula* and *B.tetracolum* following this modification of the data. The modified type 1 response times are presented in Table 4.6.

Bembidion quadrimaculatum, *B.lampros* and *B.lunulatum* are the three species with the shortest mean times for an encounter followed by a type 1 response, with times under 0.5 seconds although only 2 individuals of *B.lampros* were trapped in this experiment. The longest mean time for such an encounter was for *Notiophilus biguttatus* (2.99 ± 1.16 seconds).

The results are presented in graphical form in Figs. 4.3 and 4.4 for all species except *Agonum muelleri* except that response times greater than 10 seconds are not included. It is clear from these bar

charts that there is a proportional shift to the left (shorter response time) for a type 1 response time when compared with the type 2 response time for all species except *Bembidion tetracolum*.

TABLE 4.6

Response times for species studied in experiment 2

SPECIES	No.INDIV.		RESPONSE TIME (sec.)		p
	T	A	T	A	
<i>B.guttula</i>	7	18	1.40 $\pm$ 0.61	2.54 $\pm$ 0.54	N.S.
<i>B.quadrimaculatum</i>	21	37	0.25 $\pm$ 0.06	1.57 $\pm$ 0.39	**
<i>B.lampros</i>	2	17	0.47 $\pm$ 0.16	2.39 $\pm$ 0.41	***
<i>B.lunulatum</i>	8	15	0.49 $\pm$ 0.16	3.86 $\pm$ 0.84	***
<i>N.biguttatus</i>	22	113	2.99 $\pm$ 1.16	6.13 $\pm$ 0.66	*
<i>B.tetracolum</i>	5	11	2.28 $\pm$ 1.06	1.77 $\pm$ 0.99	N.S.
<i>L.pilicornis</i>	39	34	0.78 $\pm$ 0.19	1.46 $\pm$ 0.18	**
<i>A.muelleri</i>	9	29	0.92 $\pm$ 0.43	3.70 $\pm$ 0.87	**
<i>P.melanarius</i>	79	14	1.33 $\pm$ 0.19	4.89 $\pm$ 0.83	***

***= $p < 0.001$ **= $0.001 < p < 0.01$ *= $0.01 < p < 0.05$ N.S.= $P > 0.05$

T=Trapped (type 1 response)

A=Avoided (type 2 response)

The response times for beetles subsequently trapped are modified by subtracting 0.2seconds (see text p.111-112)

Fig. 4.3 DISTRIBUTION OF RESPONSE TIMES
FOR INDIVIDUALS SUBSEQUENTLY TRAPPED

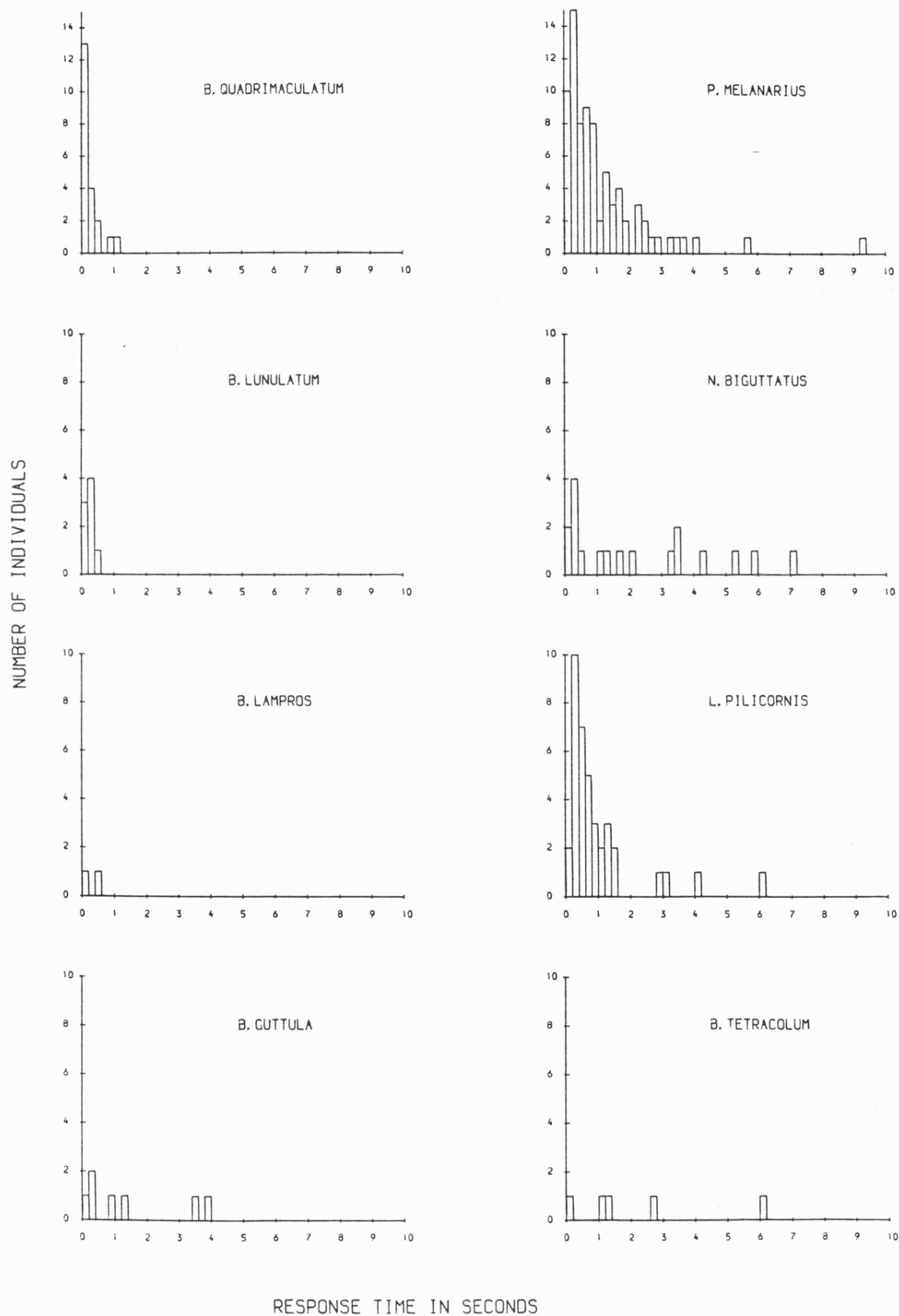
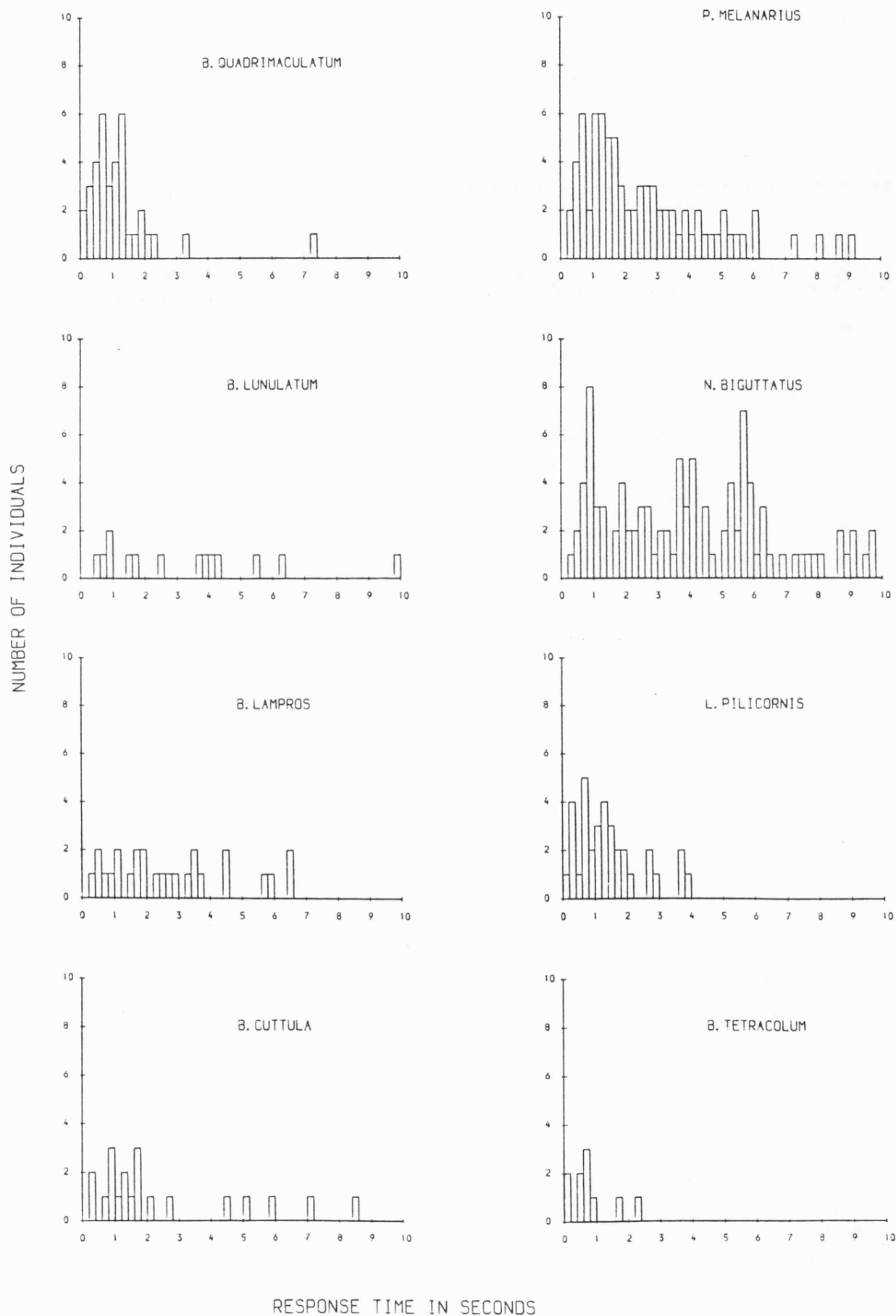


Fig. 4.4 DISTRIBUTION OF RESPONSE TIMES
FOR INDIVIDUALS SUBSEQUENTLY AVOIDING



4.2.4 Experiments 1 and 2 - Discussion

The recording technique employed in experiment 2 was much more efficient, and produced a larger body of data, than the manual technique of recording behaviour used in experiment 1. These advantages are slightly offset by the problem of coping with simultaneous encounters - the program was designed to monitor only one encounter at a time. However, the frequency of simultaneous encounters was low - approximately 3% of the total - and this is in part due to the careful choice of densities of individuals during the planning stages of the experiment.

When the results of the two experiments are combined (Table 4.3) it can be seen that sufficient individuals of all but one species, *Bembidion tetracolum*, were studied .

Analysis of the results suggests that the apparatus used did not in fact satisfy a basic assumption - that the two traps in the artificial arena were not encountered at an equal frequency. The observed differences, which are statistically significant, can perhaps be explained by the unsymmetrical positioning of the apparatus with respect to the illumination of the laboratory during both the artificial day and night. The trap nearer the monitor (trap 1) had significantly fewer encounters and this trap was also positioned slightly further away from the lights which provided illumination during the artificial day. Nocturnal individuals may have been attracted by the green light emitted by the monitor near trap 1 since this was the only form of illumination for them (the traps were positioned symmetrically with respect to the red light). Diurnal species may have been attracted by the slightly brighter illumination of trap 2 relative to trap 1 - trap 1 was shaded slightly from the fluorescent lights by the monitor - and since more

individuals of diurnal species were tested, this might explain the bias towards encounters with trap 2.

The original assumption that beetles which were captured in the field by a dry pitfall and returned to the laboratory for testing would respond in the same way as beetles collected by pooting is upheld. This suggests that beetles do not 'learn' to avoid traps, at least after only one encounter. A large number of individuals of *Pterostichus melanarius* were collected during a field weekend in Radnorshire. These were returned to Leicester, individually marked with enamel paint and the avoidance rate of the population recorded over several consecutive encounters by each individual. 272 encounters by 9 beetles were recorded and the frequency of avoidance did not differ significantly when the two halves of the duration of the experiment were compared in this respect (Chi square = 0.6, $p > 0.05$).

The relationship between beetle size and rate of avoidance is significantly correlated (this will be considered in more detail in section 4.4) but only if the two larger *Pterostichus* species are included in the analysis of the data. However, to exclude them would be an example of what Sprinthall (1987) calls a restricted range - the Pearson correlation coefficient was designed to show the strength of the relationship between high and low scores on one variable with high and low scores on the other. If either of the variables fails to contain values at the high or low end of its distribution, the resulting correlation will tend to be closer to zero than it otherwise would be. Their inclusion therefore seems to be justified since they 'represent' the larger carabids.

There is clearly a difference, for all but two of the species studied, between the time taken to respond to an encounter when beetles which are trapped are compared with beetles which subsequently avoid. One interpretation of this difference might be that beetles which are trapped are, on average, those which did not have time to respond to the encounter whereas those beetles which avoided did. This and other interpretations will be considered in greater detail in the final discussion of this chapter.

In an attempt to determine the cause of the duration of an encounter one species was studied in greater detail in the following experiment.

4.2.3 Experiment 3

For a more detailed analysis of behaviour preceding an encounter, individuals of *N.biguttatus* were studied using video techniques. Video tapes were later monitored using the time-budgeting program. This species was chosen because of its unusual behaviour at the trap perimeter (own observations discussed further in Section 4.4).

At the start of each replicate, 20 individuals of *N.biguttatus* were introduced into the arena as described in experiment 2 with the plastic cups being removed at the start of each replicate. The behaviour of these beetles was recorded for 30 minutes using a video camera with the apparatus illuminated as in expt. 1. No observer was present during the video recording of this experiment.

During playback of the video tapes, replicates were analysed using the computer program "beetle". 30 individuals were selected randomly from the tapes so that 10 individuals encountered a trap

and were trapped (criterion 1), 10 individuals encountered a trap and avoided (criterion 2) and 10 individuals did not encounter a trap at all (criterion 3).

The exact time of an encounter which satisfied one of these criteria relative to the start of the replicate could be determined from the video-tape clock. For each individual the tape was rewound exactly 60 seconds according to this clock and then the tape was played back with the behavioural changes of the beetle being recorded by the monitoring program. The program was stopped after 60 seconds for individuals in criterion 3 or as soon as beetles were trapped by (criterion 1) or avoided (criterion 2) a trap. This gave a total of 30 separate data files (one for each individual beetle) containing a sequence of behavioural changes and their respective times of occurrence.

Two types of behaviour were recorded in the first 60 seconds - walking and stationary - so that at any one time a beetle was exhibiting one of these two behavioural patterns. It was possible to extract the following information from each data file:

- A. The total time spent walking or stationary
- B. The time taken to respond after an encounter
(categories 1 and 2 only)

If the activity of an individual beetle is equated to the proportion of the total time which was spent walking, then it is possible to determine whether activity during the 60 seconds of monitored behaviour affects the chance of an encounter taking place, and whether (for categories 1 and 2) activity rate prior to an encounter in any way determines the outcome of that encounter.

Experiment 3 - Results

The method used to determine whether activity affected the outcome of an encounter (the type of response following it) was simple but one which nevertheless produced a large amount of data for analysis. The activity rate was quantified by calculating the % of time spent walking in the 60 seconds prior to an encounter.

When the hypothesis that individuals which spend a greater proportion of this time walking are more likely to encounter a trap is tested, then a significant difference is found between the mean % time spent walking (suitably transformed for statistical analysis) for beetles which did not subsequently encounter a trap (E0) and the mean % time spent walking for beetles which did (E1) (pooled results of type 1 and type 2 responses) (see Table 4.7). The sample size is 30 and so the difference between the means of 2 large samples is used (see Appendix 7). The mean time spent walking for E1 individuals was 27.43 ± 6.31 seconds ($n=20$) and this differed significantly from the mean time spent walking by randomly selected E0 individuals: 15.73 ± 7.05 seconds ($n=10$) ($t=2.83$; $0.001 < p < 0.01$). One E1 individual spent 73.58% of the time walking - a relatively large deviation from the mean. If this individual is excluded from the data on the grounds of being unrepresentative, then the difference between the means is even more significant ($t=3.18$; $0.001 < p < 0.01$) (the mean time spent walking by E1 individuals is reduced and the difference between the means becomes less, but the standard error of the altered sample is also reduced). Arriving at a value for t is slightly different in this case since the total number of individuals is less than 30 (see Appendix 7).

The individuals which did encounter a trap can be subdivided into 2 groups: those which subsequently avoided the trap (E1A) and

Table 4.7

The effect of prior activity on encounter rate and on subsequent responses

Category of individual	% of 60 sec. spent walking
E0	15.73 $\pm$ 7.06
E1	27.43 $\pm$ 6.29
E1A	20.41 $\pm$ 4.77
E1T	34.55 $\pm$ 10.79

Tabulated results of t-tests on data presented above
(% values are arc sine transformed)

Category	E1	E1A	E1T
E0	t=2.8269 df=28 **	t=1.3819 df=18 N.S.	t=3.5628 df=18 **
E1A			t=2.8386 df=18 *

Explanation:

E0 = Non-encountering individuals

E1 = Encountering individuals

E1A = Encountering individuals which subsequently avoid

E1T = Encountering individuals which are subsequently trapped

N.S.= $p > 0.05$ * = $0.01 < p < 0.05$ ** = $0.001 < p < 0.01$

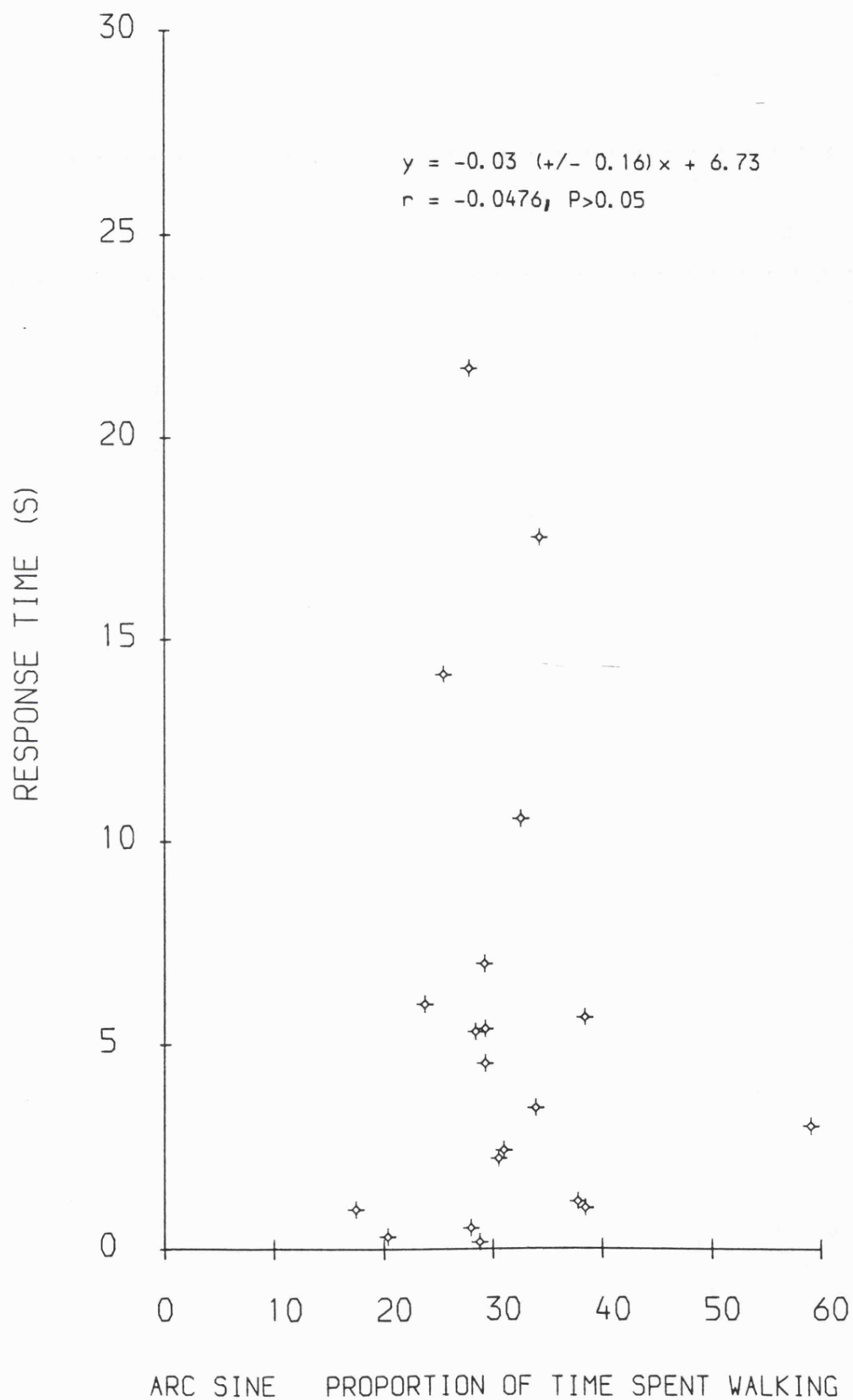
those which were subsequently trapped (E1T). There is a significant difference between the mean values for % time spent walking for the E0 individuals when compared with E1T individuals but not when compared with E1A individuals (see Table 4.7).

There is a significant difference between the means (% time spent walking) of the two encountering groups. E1T individuals spent a significantly greater proportion of their time walking prior to an encounter than did E1A individuals (see Table 4.7). In other words, beetles which are trapped following an encounter with a pitfall trap tend to be more active in the 60 seconds prior to the encounter relative to those beetles which encounter and then avoid the trap implying that activity rate prior to an encounter determines the type of response.

There is no significant difference between the mean response times of E1A and E1T individuals (these are 6.93 ± 5.72 and 4.45 ± 2.08 seconds respectively) whereas in experiment 2 a significant difference was found between these two values for the same species. It should however be noted that many more individuals were tested in experiment 2.

A further statistical test (regression analysis) was applied to the hypothesis that the activity rate of individuals (in the 60 seconds prior to an encounter) was inversely proportional to the response time (the dependant variable) of the beetle i.e. more active beetles responded to an encounter more quickly irrespective of the type of response. No significant relationship was found (Fig. 4.5). Also, when the two types of subsequent responses are treated separately in this respect then the hypothesis is still disproven. i.e. there is no significant relationship between the variables: For E1A individuals $r=0.0867$; for E1T individuals $r=-0.3106$.

FIG. 4.5
RELATIONSHIP BETWEEN ACTIVITY
AND RESPONSE TIME



Experiment 3 - Discussion

As might be expected from Brownian Theory, more active individuals should encounter traps at higher frequencies than less active individuals. Jansen & Metz (1979) showed this to be the case in a theoretical study of pitfall trapping. In the present experimental study, individuals which encountered traps (E1) were significantly more active than randomly selected individuals which did not encounter traps (E0). There is a more highly significant difference between encountering and non-encountering groups if E1 individuals are subdivided into two groups and the more active of these two groups is used in the comparison. This is because the more active of these two groups contains beetles which are subsequently trapped (E1T) and these beetles are significantly more active than individuals which encountered but subsequently avoided (E1A).

When beetles which do encounter traps are subdivided into these two groups, those which were subsequently trapped (E1T) were found to be significantly more active prior to the encounter than those which were subsequently responded by avoiding. One possible conclusion which can be drawn from such a difference is that more active beetles have less time to respond to an encounter and are more readily trapped than beetles which are moving more slowly. The significance of this is discussed in more detail in section 4.4.

The significant difference between the two encountering groups E1A and E1T (Table 4.7) suggests that prior activity determines the outcome of an encounter. However, contrary to the conclusion drawn from the t-tests, the regression of response time upon the proportion of time spent active does not give a significant relationship between

the two variables (Fig. 4.5). This suggests that activity prior to an encounter does not determine the outcome of the encounter since it is already known (Experiment 2) that beetles which are subsequently trapped have a significantly shorter response time than do beetles which subsequently avoid.

Analysis of the data from experiment 3 therefore leads to two conflicting conclusions and it cannot be stated categorically that activity prior to an encounter determines the type of response following it without testing many more individuals.

Further to this, and because *N. biguttatus* has such an unusual pattern of movement (see p.139), it would be beneficial to do a similar investigation using individuals of other species to see if any findings are upheld.

4.2.6 Experiment 4

The experiment was designed to test the relative attractive or repellent qualities of ethane diol when compared with distilled water.

To determine whether the response following an encounter was dependant on the solution used in the traps it was decided to compare the response of beetles upon encountering traps with different contents when these were presented to them at the same time in the same arena. Two variables were chosen with respect to trap content; namely 50% ethane diol (see Chapter 2), or distilled water . Any difference in the rate of avoidance of two such traps presented in the same arena would suggest that beetles are able to detect such a difference and that they are responding accordingly.

This experiment was also designed to reveal whether individuals

are differentially attracted to a particular trap initially (from beyond the trap perimeter) rather than once an encounter has commenced. Hence any difference between the two traps with respect to the rate of encounter alone, regardless of response, would suggest that the beetles were being differentially attracted to or repelled by one of the two solutions.

The control for this experiment is to present beetles with both traps identical with respect to trap content. This was only necessary for the traps containing water since the data from experiment 1 is the control for the first variable, 50% ethane diol. Individuals of two species were used in this experiment: *N.biguttatus* and *B.quadrimaculatum*.

The experiment was conducted in the same way as experiment 1, with individual beetles being removed from the arena following the avoidance of a trap, or left in the trap if they were captured. Manual records of the number of encounters were taken as well as a record of the response following an encounter.

Experiment 4 - Results

153 encounters were observed. No significant difference was found between the encounter rate with the two types of trap when presented as a 'choice' together. Similarly, the difference between the proportion of animals avoiding each of the traps following an encounter was not statistically significant even when the slight difference in encounter rate had been taken into account (see Table 4.8). The observed differences between the avoidance rates and between the encounter rates for each species, although not statistically significant, are perhaps a result of the small number of individuals tested.

The avoidance rates for the two species are consistent with the results obtained in experiments 1 and 2.

Experiment 4 - Discussion

Several workers (e.g. Luff, 1975; Adis & Kramer, 1975; Renner, 1981; Holopainen & Varis, 1986) have found that formaldehyde, even at concentrations as low as 4%, can act as an attractant when used in pitfall traps. Different species seem to be attracted to it at different rates and some not at all. Although the present investigation was limited in that only two species were tested, it does not seem that ethane diol (50% pbv) acts in the same way. The importance of close monitoring of such tests is important to eliminate the possibility that the rates of encounter with pitfall traps containing different solutions may differ. The close monitoring also allows one to be sure that beetles are not escaping from traps at different rates once they have fallen in. However, no escapes from pitfall traps were observed during the present investigation and the analysis of many hours of video records from experiment 3 where one of the most agile of carabids, *Notiophilus biguttatus*, was used, supports this finding.

One disadvantage of carrying out such experiments in the laboratory is that any effect of moving air currents which occur in the field are not taken into account. If beetles are going to detect a solution in the base of a pitfall trap then the chance of detection is likely to be increased under conditions of microturbulence.

More species need to be tested using ethane diol before the possibility that it acts as an attractant (or repellant) when used in this way can be dismissed. Such investigations must take into account the rate of encounter of traps before the number of individuals

Table 4.8 - Results of Experiment 4: Number of beetles avoiding traps
with different contents

Species	Observed Frequency Encounters with		Observed Frequency Avoidance with		Expected Frequency Avoidance with		CHI SQUARE	p
	WATER	ED	WATER	ED	WATER	ED		
	(A)	(B)	(C)	(D)	(E)	(F)		
B. quadrimaculatum	54	48	37	31	36.00	32.00	0.0590	N.S.
N. biguttatus	23	28	20	27	21.20	25.80	0.1237	N.S.

Calculation of expected frequencies for Chi squared test:

$$E = (C+D) * (A/(A+B))$$

$$F = (C+D) * (B/(A+B))$$

p = probability that beetles avoid traps at equal rates (N.S.=p>0.05)

can be compared.

4.2.5 Laboratory Experiments - Application of results to pitfall traps in the field.

The experiments carried out in the laboratory suggest that beetles avoid pitfall traps at different rates, and that such avoidance rates are species-specific. Avoidance rate seems to be correlated with body length, at least for the ten species studied, and to depend on activity immediately preceding an encounter in *N.biguttatus*.

The next step in the investigation was to see whether such findings were supported by similar experiments in the field. The experiment had to be much more simplistic for obvious reasons and to some extent artificial too in that high densities of individuals had to surround a trap at any one time in order to collect sufficient data over a short period of time. The field experiment is presented in the following section and then all five experiments discussed in more detail in the final section.

4.3 Analysis of behaviour in the field

4.31 Experiment 5 - Manual monitoring of behaviour in the field

Species studied

Five of the species which were studied in the laboratory were used also in field experiments to investigate the response of beetles to small pitfall traps. The species studied were *Pterostichus melanarius*, *Bembidion lampros*, *B.lunulatum*, *B.quadrimaculatum* and *Notiophilus biguttatus*. This choice was to a large extent determined by the availability of the insects over a short period. Individuals of the first species were collected from the study site using large dry pitfall traps and studied at night whilst individuals of all the other species were collected using a conventional pooter and studied in daylight.

Experimental apparatus and conditions

The field apparatus consisted of a small pitfall trap sunk into the soil as for the field studies (see Chapter 2), with the area immediately surrounding it enclosed by a perspex cylinder (Appendix 2 [vii]) which was sunk into the ground to a depth of 2cm. The distance between the rim of the trap and the inner wall of the cylinder was 4.75cm. 13.44% of the area of the arena was occupied by the trap (this compares with 10.61% for the area occupied by the two traps in the laboratory apparatus). Beetles which were placed within this 'arena' were unable to climb the inner walls of the cylinder or to burrow beneath it and escape from the enclosure. However, the

perspex arena often enclosed the stems of several oat plants and these were not removed. The other difference was the circular configuration of the arena in the field apparatus contrasting with the rectangular arena in the laboratory.

Experiments on diurnal species were conducted between 15.0 and 20.0°C and between 1000 and 1600 hr BST. *P. melanarius* was studied within a temperature range of 10.0 to 15.0°C and between 2300 and 0100 hr BST using a red field torch (Appendix 2 [vi]).

Living material was kept under field cage conditions and used in experiments up to 3 days after initial capture. All individuals were fed *ad lib.* on *Xenopus* pellets.

All the other experimental conditions were as those described for experiment 1 in the laboratory. All replicates were run for 30 minutes duration unless all beetles encountered the trap in less time.

Experiment 5 - Results

263 encounters were observed and recorded manually in the field (see table 4.9). Individuals of the three *Bembidion* species were occasionally observed climbing oat stems within the arena and at higher temperatures individuals of *B. quadrimaculatum* exhibited short bursts of flight activity. As a consequence of this beetles were not constantly in contact with the horizontal 'arena' as was the case in the laboratory experiments.

The rate of avoidance of the trap was calculated for each species and a Chi squared test used to compare the rates with those obtained in experiments 1 and 2. No significant difference was found between the two rates of avoidance for any of the five species which were studied both in the laboratory and in the field (Table 4.10).

Table 4.9 - Results of experiment 5

Species	No.	No.	No.	
	Trapped	Avoiding	Encounters	% Avoidance
<i>B.lampros</i>	14	37	51	72.55
<i>B.lunulatum</i>	5	18	23	78.25
<i>B.quadrimaculatum</i>	30	70	100	70.00
<i>N.biguttatus</i>	6	28	34	82.35
<i>P.melanarius</i>	48	7	55	14.58



Plate 4.2 Apparatus used in the field to determine avoidance rates. Individuals of *Bembidion quadrimaculatum* can be seen floating on the preservative fluid.

Table 4.10 – Statistical comparison of laboratory and field data

Species	A	B	C	D	E	F	Chi Square
	Number Encounters In Field	Number Encounters In Lab.	Observed Frequency of Av. in Field	Observed Frequency of Av. in Lab.	Expected Frequency of Av. in Field	Expected Frequency of Av. in Lab.	
B. lampros	51	173	37	138	39.84	135.16	0.2621 NS
B. lunulatum	23	27	18	19	17.02	19.98	0.1045 NS
B. quadrimaculatum	100	157	70	99	65.76	103.24	0.4475 NS
N. biguttatus	34	210	28	182	29.26	180.74	0.0631 NS
P. melanarius	55	137	7	22	8.31	20.69	0.2895 NS

Av. = avoidance NS = $p > 0.05$

Calculation of expected frequencies for Chi squared test:

$$E = (C+D) * (A/(A+B)) \quad F = (C+D) * (B/(A+B))$$

Regression analysis of the data with respect to the relationship between body length and rate of avoidance (arc sine transformed) produces a significant correlation: $y = -3.53 (\pm 0.72)x + 72.25$ ($r = -0.9499$ with 3 degrees of freedom $\{0.01 < p < 0.05\}$)

Once again the relationship is dependent upon the inclusion of data for the largest species (*P.melanarius*).

///

Experiment 5 - Discussion

The field investigation, although limited, supports the findings in the laboratory - at least for the 5 species which were studied under both conditions. It seems therefore that laboratory results can be applied to pitfall trap data from the field and this is useful because of the ease in which laboratory monitoring of avoidance can be undertaken.

Table 4.11 Summary of experiments showing behavioural changes
monitored and the recording techniques employed

Expt.	Species studied	Behaviour monitored			Recording Technique Employed
		Q	W	EY/ET	
1	All	NO	NO	YES	MANUAL
2	ALL	NO	NO	YES	COMPUTER
3	<i>N.biguttatus</i>	YES	YES	YES	VIDEO-COMPUTER
4	<i>N.biguttatus</i> <i>B.quadrimaculatum</i>	NO	NO	YES	MANUAL
5	<i>N.biguttatus</i> <i>B.lampros</i> <i>B.lunulatum</i> <i>B.quadrimaculatum</i> <i>P.melanarius</i>	NO	NO	YES	MANUAL

Q = behavioural category stationary

W = behavioural category walking

E = encounter with a trap

T = subsequent response type 1 (trapped)

Y = subsequent response type 2 (avoidance)

4.4 Discussion

From an analysis of 960 encounters with pitfall traps it can be concluded that beetles clearly avoid pitfall traps at differing rates in the laboratory and results suggest that this is a species specific behavioural phenomenon: If individuals selected at random from the population are allowed to encounter a pitfall trap once then the proportion of individuals captured will depend on the species. However, such a rate of avoidance is likely to be dependent upon trap design and probably upon other factors, only some of which have been investigated here (see Appendices 5 & 6).

A significant relationship between body length and avoidance rate exists, at least for the 10 species studied here (see Fig. 4.2 p.106) with smaller species within the family tending to have higher avoidance rates. The relationship is further supported by some earlier data collected in 1984. Individuals of *Pterostichus angustatus* from Timberwood Hill Plantation (see Chapter 2) were found to have an avoidance rate of 46.9% ($n=81$) under nocturnally simulated conditions identical to those described under experiment 1 in Chapter 4. The predicted avoidance rate for this species (mean body length 10.25mm [Lindroth, 1974]) is $43.9 \pm 8.4\%$. It would be a useful exercise to test predictions based on the body length of other species of similar body form from the arable ecosystem by determining their avoidance rate in the laboratory under the same experimental conditions.

Luff (1975) studied the capture efficiency of traps with respect to 6 species in the laboratory. This term, if subtracted from 100, is effectively equivalent to avoidance rate in the present study since the number of individuals captured per encounter was recorded and individual beetles were tested only once. The calculated avoidance

rates from Luff's (1975) data range from 20% to 46.7%. This range is narrower than the range found in the present study and this is probably because Luff (op. cit.) studied species which represented a narrower range of body lengths: *Nebria brevicollis*, *Harpalus rufipes*, *Pterostichus melanarius*, *P.niger*, *Agonum dorsale* and several species of *Amara*. Analysis of the data presented in his Table 7 gives no correlation between avoidance rate and body size and indeed the largest species, *Pterostichus niger*, has the highest avoidance rate and the smallest species (*Amara* spp.) the lowest. An explanation for the conflicting nature of these results, when compared with those from the present study, might be that all species (some of which are nocturnal) were tested in normal daylight (in the present study nocturnal species were not). The type of trap used to test capture efficiency differed from the small traps used in the present study and Luff (op. cit.) shows in the same paper that particular types of traps selectively capture beetles according to body length. It should also be pointed out that the species with relatively high avoidance rates in the present study (*Bembidion* and *Notiophilus*) were not studied by Luff (op. cit.).

The actual avoidance rates from Luff's study can not be compared directly with those from this study, or with predictions based on body length because both the type of trap used and the conditions under which beetles were studied are different.

There are several possible explanations to account for the relationship between avoidance rate and body length (Fig. 4.2, p.106), some of which are supported by experimental evidence. Individuals of larger species tend to have a greater velocity and a more constant pattern of movement - analysis of walking behaviour in the laboratory and of activity patterns in the field support this

(see Chapter 5). It follows that if an encounter with a pitfall trap takes place then beetles travelling at relatively high velocities will have less time to respond to the trap perimeter before the centre of gravity of the insect has passed beyond a critical point after which the beetle cannot recover its momentum sufficiently to retain a hold on the trap perimeter. Beetles which are relatively agile are occasionally able to recover once this critical point has been passed but larger beetles tend to be less agile and therefore more likely to be trapped as a consequence. Smaller species are also able to respond to the encounter before this critical point is reached because of their relatively low velocity but also because their antennae are closer to the substrate and more likely to detect the trap perimeter (J.Spence pers. comm.) (see also Appendix 6).

Adis (1979) reviews the problems associated with the interpretation of pitfall trap data and lists 18 factors which influence the sampling effectiveness of traps. One of these refers indirectly to the phenomenon of pitfall trap avoidance and he suggests that large carabids are more likely to be captured by pitfall traps due to their greater weight and higher running speed. The situation is analogous to a human being at the wheel of a motor vehicle: the margin for error is inversely proportional to the speed and weight of the vehicle. The experimental results of the present study support Adis' hypothesis.

As well as being slower, individuals of the smaller species had a more sporadic pattern of movement (own observations). This is most noticeable in the diurnal species *N. biguttatus* which exhibits frequent short bursts of activity. These have a frequency of approximately 20/minute and mean duration of 0.4 seconds (see Chapter 5). The species is a predator of Collembola and it is thought that

this pattern of activity has evolved as part of its hunting strategy (Bauer, 1979). Such a pattern of movement is suited to the detection of objects such as pitfall-trap edges. In addition to this, the acute vision of *N. biguttatus* may explain why it has a higher avoidance rate than would be expected for its size and a higher avoidance rate than other smaller diurnal species which feed on more sedentary prey and have a more uniform pattern of locomotion as a consequence. Presumably individuals of this species are able to detect the trap more easily although this advantage might be slightly offset by the relatively short antennae (but see Appendix 6).

Stating that the species has a higher than expected avoidance rate is open to question. Values of rates of avoidance (the dependant variable) predicted from body length (the independant variable) yield, in theory, the most probable rate of avoidance exhibited by a beetle of a particular length. Such a method will not, however, always produce a practical or useful prediction for a variety of reasons. Firstly, species differ in ways other than body length. It might be expected, for example, that nocturnal species will have lower than expected rates of avoidance since they will be less able to detect and avoid traps when compared with diurnal species of the same body length. Such a comparison is not possible using the data from this study but to test such an hypothesis would be worthwhile. Other factors such as patterns of movement, as discussed above with respect to *N. biguttatus* might also influence the rate of avoidance. Predictions of rates of avoidance will only be more accurate therefore if other factors are taken into account. Body length, though, is nonetheless a useful parameter with which to begin.

Luff (1975) found that relatively small carabids are more likely to be trapped by small traps like the ones used in the present study and so it should be stressed that this relationship might only be

significant when applied to this particular size or design of trap.

Some beetles were clearly captured even after sufficient time has elapsed for them to avoid the trap (when they have not passed the critical position discussed above). Although such encounters were not studied separately it can be postulated that beetles are still trapped from such a position because:

1. They are attracted to the moisture gradient which has its origin in the solution within the trap.
2. They are attempting to escape from the arena.

Avoidance rates after such encounters are also likely to be higher in smaller species due to the relative 'danger' of the drop (J.Spence pers. comm.).

It has been demonstrated (Thiele, 1977) that nocturnal species of Carabidae tend to be larger than diurnal ones. The visual image of a white plastic trap will be poorer in individuals of nocturnal species and the possibility of an avoidance response occurring will therefore be less likely. Of the 10 species studied here, the largest species are both nocturnal (*P.melanarius* and *P.niger*). All of the smaller species studied are either diurnal or 'plastic' with a bias towards diurnal periodicity (see Chapter 3).

An analysis of response times (the time elapsed between encountering a trap and responding to it) revealed significant differences between the times of the two types of response in most of the species studied. Once the observer's delay in recording a type 1 response (beetle trapped) had been taken into account these differences became even more marked. These results suggest that the

individuals' reaction to the encounter is an important factor in determining its outcome and that where the insect has sufficient time to react, it will usually avoid the trap.

The observation of many encounters reveals species-specific peculiarities which are not revealed by the data alone. The longest times recorded for a type 2 response (avoidance) are from encounters by individuals of *N. biguttatus*. This species is clearly the most agile of the carabids studied and direct observations coupled with video analysis of its behaviour during encounters show that individuals are able to pass the critical point with respect to their centre of gravity and even walk around the inner wall of the plastic cup just below the trap perimeter. Individuals usually achieve this by maintaining contact with the trap perimeter with the legs of one side of the thorax. Several encounters were observed where individuals passed the critical point but maintained contact with the perimeter using the tarsi of both hind legs. Only rarely were individuals able to recover from this position but such recoveries were only observed in this species (see Plates 4.3 a-c).

When the proportional distribution of type 1 response times for individuals of *N. biguttatus* is presented in graphical form (Fig. 4.3; p.115) it is still not clear that the pattern is a bimodal one. Observations suggest that individuals were either trapped 'immediately' i.e. they did not have time to respond to the encounter, or there was a slight delay before the insect was trapped. Although no record was taken of the type of type 1 response it is assumed that the longer times are a consequence of a delayed response but that there is an overlap of times for the two types of E-T responses.

Of these delayed responses there are also two types according to my observations. First, insects which pass the critical point but



Plate 4.3a

Notiophilus biguttatus encountering a pitfall trap. The hind tarsi are in contact with the trap perimeter. The beetle is capable of avoiding capture from this position.

Plate 4.3b

The same individual approximately 2 seconds later. The beetle is able to walk along the inner edge of the trap by maintaining contact with the trap perimeter with the meta- and meso-tarsi of one side of the body. Avoidance is still possible.



Plate 4.3c

The same individual approximately 0.5 seconds later. The beetle has lost contact with the trap perimeter and will be trapped from such a position. Contact with the ridges on the inner wall of the trap can be maintained for only a few seconds

momentarily maintain contact with the trap perimeter. They are unable recover from this position and are subsequently captured. Secondly, those insects which are captured from a position from which they could have apparently recovered, the reasons for which are not clear but two have been postulated above.

The results from experiment 3, Table 4.7 suggest that the response following an encounter might be dependent on the activity of the individual prior to that encounter. This statement is true for individuals of *N.biguttatus* when activity is quantified in the way described. It was argued above that interspecific differences in velocity might partly explain the variation in the rate of pitfall trap avoidance. Because no significant relationship was found between the proportion of time spent active prior to an encounter and the time taken between encounter and response (Fig. 4.5), I suggest that only tentative conclusions can be drawn from these results and cannot state categorically that avoidance rate is dependant on activity in all species. A more detailed analysis of the behaviour of an individual prior to an encounter is required and perhaps one with a more secure method of quantifying activity. It may be necessary to study activity in a much shorter time interval, such as one second before an encounter.

The limited investigations of experiment 4 suggest that 50% ethane diol is neither attractive nor repellent to individuals of the two species studied when compared with water and that this applies both before and during an encounter with a pitfall trap i.e. beetles are not differentially attracted to the solution from a distance, or once an encounter with the perimeter of a trap has occurred. Other workers have found that low concentrations of formaldehyde in pitfall traps can act as an attractant to some species of Carabidae but the

extent to which these results are affected by the differential capacity of species to escape from pitfall traps is still not known. Formalin is known to be more toxic to beetles than many other solutions used in pitfall traps against which it is tested and since the rate of escape from a pitfall trap is likely to increase with the time the beetles remain alive in the solution (Petruska, 1969), it is possible that the results cited above are misleading. Laboratory experiments such as experiment 4 above, which monitor the rate of encounter with traps, overcome the problem of interpretation of results where the only available data are the number of dead beetles in the trap at the termination of the experiment. It is important to record the number of individuals captured as a proportion of the total number of encounters.

The apparatus used in the laboratory is not suitable for all species of Carabidae. Individuals of *Demetrius atricapillus* collected from winter wheat in Billesdon, Leicestershire (see Chapter 2) were able to climb the inner vertical plastic boundary of the arena and would not readily encounter the traps.

The results from experiments in the field support the findings from the laboratory with differences of only a few percent when the avoidance rates from the two experiments are compared. The use of this technique in the laboratory therefore seems valid. The slight differences which do occur are likely to be due to chance alone.

If beetles in the laboratory are attempting to escape from the low humidity level and the artificial environment they might be trapped more readily than in the field where conditions in the arena are more favourable and the trap is more easily detectable due to the greater contrast between it and the substrate. This, however, is not supported by the data - there are no significant differences between

laboratory and field avoidance rates for any one of the five species studied under both regimes.

The application of the results to data from long term field studies using pitfall traps becomes less meaningful if the condition of traps in the field is allowed to deteriorate. For instance, if the trap perimeter is not kept flush with the surrounding soil then the avoidance rates exhibited by species might well be affected. Mitchell (1963) reported that traps can readily become inefficient, and especially after heavy rain and during hot dry weather. Under the former conditions mud can get splashed on the inner surface of the trap allowing beetles to grip more readily and thus increase the chance of avoidance. In hot weather the soil surrounding the trap often dries up leaving a gap next to the periphery of the trap. The rate of encounter with such a trap will therefore be biased towards larger individuals. However, Mitchell (*op. cit.*) bases his conclusions on the observation that the size of the catch decreased under such conditions. It is possible that reduced activity was responsible for the lower catch rather than reduced efficiency of the traps. The term efficiency, when applied to pitfall traps can be misleading. It is most meaningful when it is taken to mean the number of individuals captured per encounter. Many authors take it to mean the number of individuals captured regardless of encounter rate.

Careful attention to trap maintenance can reduce problems such as the ones hypothesized above. Other factors such as the presence or absence of trap covers (see Appendix 5) and the depth and concentration of the solution in the trap should also be kept constant.

CHAPTER 5

Activity

5.1 Introduction

The second main behavioural parameter which determines the number of individuals of a species which will be captured by a pitfall trap is the locomotor activity of individual beetles. All other things being equal, the chance of encountering a trap will be proportional to the mean velocity of individual beetles. It has been argued in this thesis that the chance of being captured once an encounter has occurred is independent of prior activity although this was not conclusively shown to be the case in Chapter 4 for *Notiophilus biguttatus*.

Thiele (1977) made close observations of velocity in the laboratory by timing beetles travelling a linear distance of 30cm without stopping. Velocity was presented in cm/s for 14 species from contrasting habitats. *Pterostichus melanarius*, the only species common to both studies, was found to have a mean velocity of 8.9 cm/s.

Brunsting (1983) carried out a more detailed investigation in the laboratory but only on one species: *Pterostichus oblongopunctatus* Fab. Direct and indirect observations of beetles' positions with respect to a coordinate grid were made. From these observations the velocity and pattern of movement of individual beetles could be determined. Data ranging from 0.93 to 2.22 m/hr (=0.026 to 0.062 cm/s) was presented for observations at 20°C. These estimates of velocity, however, included stationary periods of up to 30 seconds duration, and so are not comparable with the results of Thiele (1977)

cited above, who also studied this species.

Brunsting (1983) simulated the patterns of movement on a computer (angles of deviation were recorded in addition to velocity) and the number of beetles 'trapped' compared with field results of the numbers of beetles which were released and trapped in enclosures containing pitfall traps. Close agreement was found between the two sets of results.

Locomotor activity in the Carabidae has only rarely been closely studied in the field. It is usually studied indirectly by using pitfall traps (which can only give a relative estimate) but it is clear from the previous chapter that pitfall traps cannot be used to make interspecific comparisons in this respect unless the avoidance rate of traps is taken into account.

Rivard (1965) estimated the dispersion rate of beetles in the field by calculating the distance between the points of release and recapture of marked beetles (using pitfall traps) where the approximate time interval between the two observations was known (i.e. the linear distance). Using individuals of *P.melanarius* he found values ranging from 2.29 to 18.29m per night for this parameter but no traps were located more than 18.29m from the point of release and so beetles which did not encounter the traps and travelled greater linear distances would not have been detected.

The same technique was used by Kirchner (1960); Mitchell (1963) and Neumann (1971) (cited in Thiele, 1977). Mitchell (1963) found that *B.lampros* travelled between 0.15 and 10m (mean 1.6m) in 1 day. Kirchner (1960) reported that *P.melanarius* travelled up to 15m in one night (mean distance = 3m). Much higher values were reported by Neumann (1971) for *Carabus problematicus* Herbst (2 individuals travelled 70 and 77m in one night) but this is a forest species and individuals were released in fields. Again, these values represent

the shortest distance between the points of release and recapture and are therefore underestimates of actual distance travelled. In all these studies, the time between observations was at least several hours.

In simulation studies, Kitching (1971) demonstrated a negative exponential type drop off in the number of animals detected in sites relatively far away from the point of release and these findings agree with field observations on the ceratopogonid *Culicoides impunctatus* Goet. (Diptera) (Kettle, 1951). Another problem with using pitfall traps therefore, is that beetles travelling relatively long distances will be underrepresented in traps. The chance of encounter decreases with distance (due either to an increased distance between traps or to a lower relative proportion of animals to traps since of those released, some will have been captured by the inner traps). Alternatively, the underrepresentation might be a manifestation of the fact that marked beetles which travel relatively long linear distances have left the sampling grid altogether. Sampling will thus be biased towards beetles maintaining a local position with respect to the point of release, and thus towards beetles which travel relatively short linear distances. Other beetles entering the grid from outside do not compensate for this since they are not marked.

Despite these problems such estimates do give an indication of the distances beetles are capable of traversing and form a basis for comparison with the data presented in this chapter.

Baars (1979b) used radioactive tracers to determine patterns of movement of *Pterostichus versicolor* (Sturm) and *Calathus melanocephalus* (L.) in the field. Beetles' positions were located every 24 hours with the aid of a Geiger counter and thus the use of pitfalls was avoided, but once again the time interval between observations was relatively long.

Only Heydemann (1957) presents realistic field data on velocity where the time interval between observations was small or observation was continuous. Large species (e.g. *Carabus cancellatus* Ill. and *C. auratus* L.) covered distances ranging from 1.8 to 2.3 m/minute in arable fields. (These data will be discussed further later in the chapter {p. 192}).

Thiele (1977) reported that the distance covered by an adult carabid beetle in its lifetime (i.e. the linear distance between its position at emergence and at death) depends on its size. Den Boer (1981) reported that individuals of *P. versicolor* covered less than 200m in an adult lifetime and that the distance for individuals of the smaller *Calathus melanocephalus* was less than 80m. Again these distances do not relate to velocity since they are based on two observations only but there seems to be a relationship between distance and the body size of a beetle.

Baars (1979b) found that the mean distance covered between observations of individual beetles depended on ambient temperature at soil level and that this distance was also inversely proportional to the amount of precipitation. However, there is no direct evidence from the study that locomotor activity was reduced or enhanced under such conditions since the possibility that beetles moved at the same velocity but changed direction more frequently and remained near the last point of observation was not examined and hence cannot be discounted.

Simple empirical studies of beetles show that they rarely travel in straight lines and so studies in which long time intervals are left between observations will tend to underestimate velocity. To estimate velocity more accurately an experimental strategy which involves almost continuous monitoring of patterns of movement is

necessary. Such a strategy takes into account changes in direction which also go undetected when the time between observations is long.

The second major parameter then, in addition to velocity, is the relative change in direction made by an animal. Velocity and directionality combined make up the pattern of movement of an epigeic insect (Baars, 1979b) or indeed of any animal (Siniff & Jessen, 1969). Baars (1979b) defines two patterns of locomotion in carabid beetles: random walk and directed movement which can be described in terms of relative changes in direction per unit time. Random walk involves relatively more changes of direction per unit time with the result that the beetle remains in a relatively smaller area - perhaps one which is a profitable prey patch. In the directed movement phase, the pattern of movement of the beetle more closely resembles a straight line since there are fewer changes of direction per unit time and might be characterized, according to Baars, by hungry beetles searching for an aggregation of prey. He could find no fixed predictable pattern of alternation between the two but hypothesized that the degree of hunger might be a determining factor.

In computer simulations using field data, Baars (1979a) found that the simulation of directed movement resulted in significantly more encounters with pitfall traps than when random walk was simulated. Like Brunsting (1983), he found close agreement between captures from simulations and actual pitfall captures in the field.

The aim in this part of the study was to determine the movement patterns of four species of Carabidae in the field over much shorter periods of time than had previously been attempted in the field and, if possible, to relate these to body length. These data would then be used in simulation experiments along with data on avoidance rates to determine the probability of capture of an individual by a grid of

pitfall traps.

5.2 Materials & Methods

Of the five species of Carabidae that were studied with respect to locomotor activity in the field, three were diurnal: *Notiophilus biguttatus*, *Bembidion lampros* and *B. quadrimaculatum* and one nocturnal: *Pterostichus melanarius* (see Chapter 3). These particular species were chosen because estimates of population density and avoidance rates had already been determined and they were relatively abundant in the arable crop. In addition, *Agonum muelleri* was studied because a species of intermediate body size was required. This species was found to be plastic with a bias towards diurnalism in diel periodicity experiments. Its avoidance rate was known but no data on its absolute abundance was available.

All observations were made in the arable field between 11th June and 28th August, 1986 and between 6th May and 30th June, 1987. Diurnal species and individuals of *A.muelleri* were observed between 1000 and 1600 BST and individuals of *P.melanarius* were studied between 2330 and 0300 BST. An infrared light (Appendix 6 [i]) attached to my head was used to facilitate observation of *P.melanarius* at night.

Beetles were initially captured by using large dry pitfall traps or taken directly from the soil surface using a pooter. Where possible beetles were identified in the field using a hand lens (x10 magnification) but all identifications were checked in the laboratory after monitoring locomotor activity.

All individuals were marked by the application of a spot of white 'Airfix' enamel paint (colour G1) to the pronotum to facilitate observation. Individuals of the three smallest species were kept in

plastic petri dishes (7cm diameter) containing moist filter paper (Whatman No. 1) until the time of release and commencement of observation. Individuals of *P.melanarius* and *A.muelleri* were kept in plastic sandwich boxes (325cm² basal area) with perforated lids also containing moist filter paper.

Individual beetles were released for observation not longer than 20 minutes and not less than 5 minutes after their initial capture. These time limits were chosen to reduce the chance of increased activity in response to confinement (Greenslade, 1964) and to allow the paint to dry (Lewis, 1984) respectively. The earliest time of capture of an individual to be studied was therefore 0940 (diurnal and plastic species) and 2310 (*P.melanarius*) BST. To release beetles at random a table of previously generated random numbers was used in conjunction with the the coordinate grid based on a series of numbered pegs used for quadrat sampling (Chapter 3).

Beetles were monitored for 15 minutes from the time of their release with observations of their position being made every minute (see below). A stop watch (Appendix 2 [viii]) which emitted a sound every minute was used as a signal for this purpose. This was essential so as not to lose sight of the beetle by having to refer visually to a timing device.

Consecutively-numbered white plastic pegs (Appendix 2 [ix]) with tapered ends were used to mark the position of a beetle at each 1-minute interval. These pegs were pushed into the soil only when the beetle had moved away from its recorded position so as not to influence its activity. The first peg, peg 0, was used to mark the point of release of the beetle. The position of the beetle after 1 minute was recorded using peg 1 and so on. If a beetle did not move between observations then the next peg was discarded. After 15 minutes the beetle was recaptured and placed in a labelled tube for

subsequent confirmation of its identity. A similar method was used by Baars (1979b), but with a 24-hour time interval between the placement of pegs.

Beetles were placed in tubes containing ethyl acetate vapour and on returning to the laboratory, their body length was recorded and identification confirmed before being preserved.

The distance between consecutive pegs and the actual compass bearing of peg $n+1$ from peg n were recorded. Distances were measured to the nearest 5mm using a ruler and bearings to the nearest 5 degrees using a compass (Appendix 2 [x]). Brunsting (1983) used a similar method in the laboratory but using a coordinate grid placed between the observer and the beetles and recorded velocity in 3cm



Plate 5.1 White plastic pegs relating to the movement pattern of an individual beetle in the field.

steps and changes in direction to the nearest 10 degrees as they occurred.

Records of the temperature at the start and finish of the 15 minute observation period were made and the mean temperature for the observation of any one individual was taken to be the mean of the two readings. All data were subsequently transferred to the VAX mainframe computer for analysis.

Data from the detailed study of activity of *Notiophilus biguttatus* in the laboratory (Chapter 4) using a video camera and the time budgeting program 'Beetle' were also used to explain some of the results from the field.

5.3 Results

Despite the precautions taken, several individuals which were released were lost during the 15 minute observation period leaving several truncated sets of data. This occurred particularly at night due to the low level of illumination provided by the infra-red light. 9 complete sets of data were eventually obtained for both *P.melanarius* and *N.biguttatus*. 6 sets were obtained for each of the two species of *Bembidion* and 4 sets for *A. muelleri*.

All tables (pp.167-177) and figures (pp.178-187) are presented in order at the end of section 5.3.

Movement patterns

Graphical representations of patterns of movement are presented for individuals of two species (Figs 5.1 - 5.3): *B.lampros* (Ref. A97) and *A.muelleri* (A03 & A09). (Parenthesized reference numbers are individual specific and were allocated to all individuals which were monitored in the field {see Table 5.5}).

These patterns were produced by the mathematical simulation of movement on the VAX mainframe computer, which will be discussed in greater detail in Chapter 6. When the scale is taken into account, they reveal the distance moved and the angle of deviation between observations. (The diagrams give the impression that beetles moved between positions in straight lines but this is not the case because beetles' positions were only recorded every minute).

None of the individuals represented showed a particularly directed pattern of movement (Baars 1979a) since several changes of direction greater than 45° occurred within the space of 15 minutes. However, the present study is on a much smaller time scale than that of Baars (1979a) whose time between observations was 24 hours.

The linear distance between the points of release and recapture is less than the estimated total distance travelled in each case (the sum of the linear distances between consecutive observations) although this was liable to considerable variation.

In agreement with the findings of Siniff & Jessen (1969) working on patterns of movement in mammals, no mathematical relationship could be found which allowed individual patterns of movement to be quantified and compared although this was attempted. Instead, the movement pattern must be broken down into components such as actual distance, linear distance, and deviation per unit time. Each of these components will be considered below along with other results which come out of analysis of the data.

Actual distance

In this study, actual distance is defined as the total distance travelled by beetles between the first and last observations in the field i.e. in 15 minutes. This is simply the sum of the distances recorded between consecutive pegs in the field. This will still

be an underestimate of the true actual distance travelled because the path taken between consecutive pegs is not necessarily the shortest distance between them and deviations from a straight line go undetected. Similarly, a beetle could, theoretically, be further away from peg n at some time between the n th and $n + 1$ observations than when the $n + 1$ observation of its position is made. The simplest case of this would be if the beetle travelled in a straight line and made one 180° turn at some time between the observations.

Accuracy is sacrificed to the necessity to set a lower limit on the time interval between observations (a limit to the number of pegs per unit area is one reason). To overcome this it is necessary to make an assumption: that beetles travel between successive observations in a straight line. However, the level of inaccuracy is relatively small and is certainly less than in the other field studies discussed above.

The frequency distribution of actual distance is presented for each species in Fig. 5.4 (data of conspecific individuals combined). If only minutes in which movement occurred are considered i.e. when distance between observations is $>0\text{mm}$ (no situation occurred in the field where an individual beetle moved from one position and back to the same position within 60 seconds), the distribution is only clearly unimodal in one case: *N.biguttatus*.

The mean actual distances travelled for each species are presented in Table 5.1. These range from 512.78mm ($=34.19\text{mm/min.}$) for *N.biguttatus* to 1942.78mm ($=129.52\text{mm/min.}$) for *P.melanarius*. t-tests on these data (Table 5.2) reveal that the means are significantly different for all possible comparisons except for *B.quadrimaculatum*/*N.biguttatus*.

N.biguttatus, which travelled the least mean actual distance in

15 minutes, is not the smallest species but, when the data for individual beetles are considered, the interspecific range of actual distances is greater (Table 5.5): from 180mm (*N.biguttatus* A73) to 3455mm (*P.melanarius* A83). It is apparent from these data that the actual distance travelled by beetles in 15 minutes increases with increasing body length. When this is tested statistically i.e. when actual distance is regressed upon body length, then the relationship is a significant one (Table 5.6; Fig. 5.6).

When the same hypothesis is tested intraspecifically, however, the relationship is not significant for any of the 5 species (Table 5.8). It should be noted that the sample sizes are small and the range of values for the independent variable is very narrow for each species i.e. there is a 'restricted range' (Sprinthall, 1987).

Support for the finding that actual distance is dependent upon body length comes from a statistical analysis of the data presented by Thiele (1977). If the mean velocity of species presented by him is regressed upon body length then a significant positive correlation between the two variables is found ($r = 0.7216$ for 9 d.f.; $0.01 < p < 0.05$). Lindroth (1974) presents ranges for body length for 11 of the 14 species presented by Thiele (1977), and the mean of these values was taken (or mean values from my own data where applicable) for the regression. The range was from 7.10mm (*Agonum dorsale* Pont.) to 17.52mm (*Pterostichus niger*). Thiele (1977) also argues that the mean distance travelled by an adult carabid beetle in its lifetime is likely to be dependent upon its size. Experimental support for this hypothesis comes from the studies of Baars (1979b) and Niemelä et al. (1986).

The regression equation derived from my own data and presented in Fig. 5.6 can be used to predict the actual distance of a species for which independent data is available from the literature (e.g.

Brunsting (1983) for *P.oblongopunctatus*) and of which the mean body length is known (Lindroth, 1974). The predicted distance for this species (11.05mm long) is 6.06 ± 0.78 m/hr. Brunsting (1983) found that individuals moved distances ranging from 0.93 to 2.22 m/hr.

Linear distance

Linear distance is defined as the shortest distance between two consecutive observations of a beetle's position. In this study the term refers to the distance between the point of release and the final observation of a beetle's position 15 minutes later.

The linear distance travelled by each individual between the first and last observations was not recorded in the field but can be derived from the original data set by successive calculation of coordinates after each move and then calculating the distance between the first and last positions using Pythagoras' Theorem. If the position of a beetle at time t is represented by the coordinates X_t, Y_t then its position at time $t+1$ minute is calculated as follows:

$$X_{t+1} = X_t + (\cos(A)*D)$$

$$Y_{t+1} = Y_t + (\sin(A)*D)$$

where A is the bearing of the position at time $t+1$ relative to the bearing at time t and D is the distance between the two positions. After repeating this calculation 15 times the linear distance can be calculated as follows:

$$\text{Lin. dist.} = (\{X_{t+15} - X_t\}^2 + \{Y_{t+15} - Y_t\}^2)^{\frac{1}{2}}$$

The mean linear distance is presented for each of the 5 species (Table 5.1). Once again *P.melanarius* has the highest mean value and

N.biguttatus the lowest. t-tests on these data (Table 5.2) reveal significant differences between *N.biguttatus* and all other species except *B.lampros*. The other interspecific comparisons reveal no significant difference in this respect.

Despite the apparent increase with increasing body length, there is no significant interspecific linear relationship between linear distance and mean body size when conspecific data is pooled although the correlation coefficient is relatively high ($r=0.7637$, d.f.=3). This is perhaps a combination of the fact that the linear distances of species overlap in most cases (the means are not significantly different) and because of the low number of cases.

The linear distances moved by individual beetles in 15 minutes in this study range from 22.04mm (*N.biguttatus* A42) to 1.21m (*P.melanarius* A89) (Table 5.5). The data reveal that some individuals clearly travelled actual distances which were many times greater than the linear distance - most noticeably *P.melanarius* A83 where the ratio of actual linear distance was almost 37.

The interspecific relationship between linear distance and body size is significant (Table 5.6; Fig. 5.7). Once again however, there is no significant intraspecific relationship (Table 5.7).

Baars (1979a) found that individuals of *Pterostichus versicolor* and *Calathus melanocephalus* moved linear distances ranging from 4.0 to 14.3 m/day and from 0.9 to 3.9 m/day respectively. Baars (op.cit.) points out that the mean distances covered by *C.melanocephalus* was approximately 0.6 of that of *P.versicolor* which closely resembles the body length ratio of the two species (7.4mm:10.6mm). The predicted linear distances for these two species from the present study is 21.48 ± 4.88 m/day (*P.versicolor*) and 17.63 ± 3.40 m/day (*C.melanocephalus*). These calculations are based on the assumption that beetles are active for only half of the 24-hour period. If the

mean of the data presented by Baars (op.cit.) is taken for each species then the predictions are approximately 2 and 5 times greater than the observed values respectively. The significance of this difference will be discussed later (p.191).

Finally there is a significant positive correlation between linear distance and actual distance (Table 5.6) i.e. as the actual distance travelled increases so does the distance between the points of release and recapture, irrespective of the angle of deviation between observations. The significance of this was discussed above with respect to actual distance (in effect, distances quoted by other authors are linear distances since the time between observations is great).

Proportion of time spent active

The number of consecutive minutes spent without movement occurring can be determined from the data set. This can be seen by calculating the sum of the difference between the time of consecutive positions which are joined by a line in Figs. 5.1 - 5.4 where this difference is greater than 1 minute. For example, *N.biguttatus* A70 remained stationary for at least 120 seconds between the 11th and 14th minute from the time of release. The mean number of minutes during which movement occurred (hereinafter referred to as the number of active minutes) is presented for each species in Table 5.1. t-tests on these mean values (Table 5.3) give significant differences between *P.melanarius* and all other species, but not between the other species. However, the number of active minutes is significantly positively correlated with body length (Table 5.6; Fig. 5.8). There is no significant intraspecific relationship (Table 5.7) probably because of the very restricted range of lengths in each species.

Brunsting (1983) found that 3.1 to 8.5% of individuals of *Pterostichus oblongopunctatus* were active at any one time. In the present study, the % of minutes which were positive for activity ranges from 52.2 to 82.2. These values are much higher but there are at least two explanations for the differences observed. First, the technique employed here was not as accurate since any short burst of activity in 1 minute is taken to mean the beetle was active for the whole minute. So, for example, a beetle moving for only 5 seconds in 1 minute is active for only 0.5% of the 15 minute period but the method employed registers this as 6.7%. In support of the present investigation Brunsting (1983) worked at high densities of individuals and the low level of activity may have been a response to overcrowding in that intraspecific encounters were avoided.

Even so, the parameter is of limited use since it tends to overestimate the proportion of time spent moving.

Mean velocity

The mean velocity for each species is presented in Table 5.1. This is defined, for each individual, as the ratio of actual distance travelled to the number of active minutes. Mean velocity is calculated this way, and not by dividing actual distance by 15, because it more closely represents the true mean velocity of a beetle when it is moving. The estimates may still include stationary periods of up to nearly 120 seconds since only whole minutes characterised by no activity are excluded. (The stationary periods can be longer than 60 seconds because a beetle could stop after x minute + 1 second and not move again until 2 seconds before $(x+2)$ minutes. This hypothetical beetle would thus have been stationary for 117 seconds but each 60 second period would be recorded as one in which movement had occurred).

As might be expected from the relative size of individuals, *P.melanarius* had the highest mean velocity. t-tests (Table 5.3) reveal significant differences between the means of most species but not between *P.melanarius* and *A.muelleri* (the two largest species) nor between *B.lampros* and *B.quadrimaculatum* (the two smallest).

The highest and lowest mean velocities recorded for individual beetles (Table 5.5) were 32mm min^{-1} (*N.biguttatus* A74) and 246.79mm min^{-1} (*P.melanarius* A83). When velocity is regressed upon individual body size then the relationship is a significant linear one (see Fig. 5.9). This might be expected since mean velocity is simply actual distance divided by the number of minutes spent active which showed little difference when the means for each species were compared (Table 5.3).

The linear relationship between body length and mean velocity is not significant when intraspecific data is considered (Table 5.7).

Brunsting (1983) is the only other worker to estimate velocity in this way since Thiele (1977) gives absolute estimates of velocity. Brunsting (1983) worked on *P.oblongopunctatus*, which, according to Lindroth (1974), has a body length of 11.05mm. Its predicted mean velocity from the regression equation, would be 130.59 mm/minute (range with standard error = 116.01 to 145.18mm/minute). Brunsting presents data ranging from 0.93 to 2.22 m/hr at 20°C which is equivalent to 15.5 to 37 mm/minute. However, in a footnote to his Table II he states that "The short (<30 second) halts are included in these figures. They take up about 2/3 of the measured timeThus the actual speed of locomotion is about 3 times as high ..." If this is taken into account (46.5 to 111 mm/minute) then the prediction is reasonably accurate.

Brunsting (1983) found a relationship between mean velocity and ambient temperature for *P.oblongopunctatus*, and also that the

duration of periods of activity increase with temperature in this species. No such relationship was found in the present study when intraspecific data were analysed but sample sizes are small (Table 5.8).

Angle of deviation

The angle subtended by peg $n+1$ with respect to the line between peg n and peg $n-1$ represents the angular deviation of beetles in degrees/minute. The frequency distribution of deviation between observations is presented for each species (Fig. 5.5). Green & Pointing (1962) present similar distributions for patterns of movement in *Rhyacionia buoliana* (Schiff), the European pine shoot moth, and so too does Kitching (1971) for the flour beetle *Tribolium confusum* Jacq. The distribution pattern seems to be common to many animal species. Thus Siniff & Jessen (1969) show that this is the case for both the red fox *Vulpes vulpes* and for the snowshoe hare *Lepus americanus*.

A high proportion of observations resulted in no deviation since beetles could not deviate when no movement occurred. The proportion of deviations which occurred when beetles moved between observations is indicated by the shaded area on each bar in Fig. 5.5.

The same statistical test was applied interspecifically to the angle of deviation between observations as was applied to the difference between the mean distance, linear distance and velocity of each species. Differences between mean angles of deviation of species were not significant in each instance (Table 5.4) except for the difference between *B.quadrimaculatum* and *P.melanarius* and between *A.muelleri* and both *N.biguttatus* and *B.quadrimaculatum*. Consequently, this parameter seems not to differ interspecifically in any predictable way as far as the present study is able to ascertain.

Agonum muelleri has the highest mean deviation at 96.67° per minute and *P.melanarius* falls in the middle of the series in this respect. There seems to be less of a relationship between body length and angular deviation and when this is investigated statistically, there is no significant linear relationship between the two variables (Table 5.6).

If only minutes where movement occurred are considered, then the angle of deviation becomes a more meaningfully descriptive statistic. Mean values are presented for species (Table 5.1) and for individuals (Table 5.5). However, there is still no significant interspecific difference between the means (Table 5.4) and no significant interspecific correlation between the mean angle of deviation of individuals and body length (Table 5.6; Fig. 5.10).

Baars (1979a) found no relationship between patterns of movement and temperature and the same results come out of the present study. When the angle of deviation is regressed upon ambient temperature for *B.quadrinotatum* and *B.lampyris* (the two species with sufficient variation in the independent variable) then the correlation coefficient is not significant (Table 5.9).

There is no significant relationship between the mean deviation/move and the ratio of linear distance:actual distance (Table 5.6). This supports the findings of other workers – a low angle of deviation per unit time does not necessarily suggest that an animal is travelling in a directed way since one 180° turn can set the animal back on a path towards its original starting point (Siniff & Jessen, 1969).

A further modification of the data gives the deviation per minute for moves where the deviation between observations was greater than 0 degrees (Table 5.1). These values are presented for species

only, since the standard errors for individuals are high due to low sample sizes. *A.muelleri* has the highest value, with a mean deviation between observations of 100.5°. *A.muelleri* differs significantly from *P.melanarius*, *B.quadrimaculatum* and *B.lampros* but not from *N.biguttatus* ($p=0.054$) (Table 5.3). All other species have similar mean deviations and the only significant difference is between *N.biguttatus* and *P.melanarius*.

No comparable data on the angle of deviation in the field over such a short time period is recorded in the literature for comparison.

Table 5.1 Activity data for 5 species of Carabidae

Species	Mean actual distance (mm)	Mean linear distance (mm)	Mean no. of active mins	Mean velocity (mm/active min.) (see Table 5.5)	Mean deviation (degrees)	Mean deviation (degrees/active min.)
<i>N. biguttatus</i>	512.78 ± 94.07	184.03 ± 44.77	8.33 ± 0.71	61.53 ± 6.34	37.89 ± 4.79	72.35 ± 6.54
<i>P. melanarius</i>	1942.78 ± 238.54	551.36 ± 121.55	12.33 ± 0.53	157.52 ± 9.81	47.70 ± 4.21	58.92 ± 4.53
<i>B. quadrimaculatus</i>	611.66 ± 90.85	270.01 ± 66.14	7.83 ± 0.95	78.08 ± 7.61	26.55 ± 5.03	53.78 ± 8.31
<i>B. lampros</i>	963.33 ± 98.73	381.82 ± 78.99	10.33 ± 0.49	93.22 ± 7.11	39.83 ± 5.29	57.45 ± 6.51
<i>A. muelleri</i>	1255.00 ± 133.24	468.95 ± 144.19	9.25 ± 0.63	135.67 ± 12.26	56.96 ± 8.60	96.67 ± 9.79

Table 5.2

t-tests comparing mean actual distances moved

Species	P.m.	N.b.	B.q	B.l.
A.muelleri	2.82	4.92	3.68	1.57
	193	193	148	148
	**	***	***	N.S.
B.lampros	5.04	-3.92	2.66	
	223	223	178	
	***	***	**	
B.quadriramaculatum	7.01	-0.93		
	223	223		
	***	N.S.		
N.biguttatus	9.03			
	268			

t-tests comparing mean linear distance moved

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	0.40	2.51	1.41	0.58
	11	11	8	8
	N.S.	*	N.S.	N.S.
B.lampros	1.04	2.35	1.09	
	13	13	10	
	N.S.	*	N.S.	
B.quadriramaculatum	1.76	1.12		
	13	13		
	N.S.	N.S.		
N.biguttatus	2.84			
	16			
	*			

Format of squares: t value

degrees of freedom

Level of significance

(*=0.01<p<0.05 **=0.001<p<0.01 ***=p<0.001 NS=p>0.05)

Table 5.3

t-tests comparing mean number of active minutes
(proportion of time spent active by species)

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	3.42 11 **	0.79 11 N.S.	1.10 8 N.S.	1.36 8 N.S.
B.lampros	3.30 13 **	1.57 13 N.S.	2.16 10 N.S.	
B.quadrinaculatum	4.61 13 ***	0.92 13 N.S.		
N.biguttatus	4.53 16 ***			

t-tests comparing mean velocities of species

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	1.19 146 N.S.	5.95 110 ***	4.16 82 ***	3.22 97 **
B.lampros	4.54 171 ***	3.33 135 ***	1.44 107 N.S.	
B.quadrinaculatum	5.00 156 ***	1.65 120 ***		
N.biguttatus	7.37 184 ***			

For explanation of layout and symbols, see Table 5.2

Table 5.4

t-tests comparing mean deviation of species

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	1.09 180 N.S.	2.10 180 *	3.30 138 ***	1.88 138 N.S.
B.lampros	1.29 208 N.S.	0.15 208 N.S.	1.75 166 N.S.	
B.quadrinaculatum	3.26 208 ***	1.65 208 N.S.		
N.biguttatus	1.55 250 N.S.			

t-tests comparing mean deviation/move of species

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	3.36 72 ***	2.10 97 *	3.36 72 ***	3.46 88 ***
B.lampros	0.19 157 N.S.	1.60 121 N.S.	1.76 105 N.S.	
B.quadrinaculatum	0.58 141 N.S.	0.35 96 N.S.		
N.biguttatus	1.74 166 N.S.			

For explanation of layout and symbols see Table 5.2

Table 5.4 contd.

t-tests comparing mean deviation of species for deviations > 0 degrees

Species	P.m.	N.b.	B.q.	B.l.
A.muelleri	4.03	1.95	3.33	3.04
	126	89	66	77
	***	N.S.	***	**
B.lampros	0.58	1.29	0.74	
	145	108	85	
	N.S.	N.S.	N.S.	
B.quadrifasciatum	0.36	1.89		
	134	97		
	N.S.	N.S.		
N.biguttatus	2.19			
	157			
	*			

For explanation of layout and symbols see Table 5.2

Table 5.5 Activity data of individual beetles

Species	Ref.	Actual distance (mm)	Linear distance (mm)	No. Active mins	Mean velocity (mm/active min.)	Mean directional change/move (degrees)	Body length (mm)	Temp. °C
<i>N. biguttatus</i>	A60	680	252.74	9	75.56 ± 16.28	51.87 ± 15.12	5.65	17.0
<i>N. biguttatus</i>	A70	740	96.94	10	74.00 ± 8.12	58.89 ± 15.74	5.60	18.0
<i>N. biguttatus</i>	A72	805	257.06	10	80.50 ± 18.80	81.11 ± 19.41	5.32	21.0
<i>N. biguttatus</i>	A73	180	110.51	5	36.00 ± 4.30	97.50 ± 34.06	4.78	16.2
<i>N. biguttatus</i>	A74	230	67.64	7	32.85 ± 7.86	112.50 ± 13.95	4.95	20.0
<i>N. biguttatus</i>	A75	240	134.14	6	40.00 ± 11.97	96.00 ± 29.51	4.92	20.0
<i>N. biguttatus</i>	A42	255	22.04	7	36.43 ± 10.16	64.16 ± 24.17	5.04	19.0
<i>N. biguttatus</i>	A43	610	260.80	11	55.45 ± 11.94	57.50 ± 14.87	4.79	19.0
<i>N. biguttatus</i>	A13	875	454.40	10	87.50 ± 34.73	66.11 ± 19.67	4.80	17.0
<i>P. melanarius</i>	A81	1260	592.29	11	114.54 ± 27.43	68.50 ± 15.39	15.98	10.0
<i>P. melanarius</i>	A82	1225	150.54	10	122.50 ± 24.39	56.11 ± 14.59	14.30	10.0
<i>P. melanarius</i>	A83	3455	93.82	14	246.79 ± 23.56	53.46 ± 10.81	15.11	10.0
<i>P. melanarius</i>	A84	1580	382.47	14	112.86 ± 24.00	60.77 ± 14.03	14.02	10.0
<i>P. melanarius</i>	A85	1635	260.01	13	125.77 ± 19.54	78.75 ± 16.78	14.27	10.0
<i>P. melanarius</i>	A86	2200	835.29	11	200.00 ± 37.84	60.50 ± 12.50	14.12	10.0
<i>P. melanarius</i>	A87	2065	658.85	13	158.85 ± 27.05	57.92 ± 9.38	14.05	10.0
<i>P. melanarius</i>	A88	1530	778.03	11	139.09 ± 25.67	52.50 ± 14.65	15.00	11.0
<i>P. melanarius</i>	A89	2535	1210.98	14	181.07 ± 34.19	43.46 ± 14.86	14.25	11.0

Table 5.5 contd.

Species	Ref.	Actual distance (mm)	Linear distance (mm)	No. Active mins	Mean velocity (mm/active min.)	Mean directional change/move (degrees)	Body length (mm)	Temp. °C
B. quadrimac.	A59	830	84.31	11	75.45 ± 13.47	65.00 ± 13.68	3.41	18.0
B. quadrimac.	A71	835	438.86	10	83.50 ± 9.37	102.22 ± 19.38	3.30	18.0
B. quadrimac.	A90	775	452.73	7	110.71 ± 27.5	58.00 ± 32.12	3.70	19.0
B. quadrimac.	A91	400	293.96	5	80.00 ± 32.71	5.00 ± 2.89	3.21	12.6
B. quadrimac.	A92	390	265.22	6	65.00 ± 24.76	23.00 ± 7.39	3.22	12.7
B. quadrimac.	A94	440	84.95	8	55.00 ± 15.03	22.86 ± 8.44	3.31	14.0
B. lampros	A93	1020	184.9	11	92.73 ± 23.48	81.11 ± 18.14	3.65	16.2
B. lampros	A95	1125	468.28	9	125.00 ± 15.27	69.38 ± 18.81	3.84	18.4
B. lampros	A96	875	215.48	9	97.22 ± 14.19	61.25 ± 17.21	3.70	18.0
B. lampros	A97	760	285.27	11	69.09 ± 11.83	44.09 ± 12.48	3.42	18.2
B. lampros	A98	1325	699.37	12	110.41 ± 18.79	58.18 ± 16.13	3.60	17.7
B. lampros	A99	675	437.60	10	67.50 ± 11.21	35.55 ± 15.40	3.70	16.6
A. muelleri	A03	1380	405.82	9	153.33 ± 31.36	80.00 ± 16.26	7.32	18.0
A. muelleri	A05	1555	825.78	11	141.36 ± 21.11	96.00 ± 24.58	7.28	16.0
A. muelleri	A09	1135	515.80	9	126.11 ± 26.78	111.25 ± 15.55	7.40	19.0
A. muelleri	A31	950	128.39	8	118.75 ± 20.08	102.86 ± 19.54	7.27	18.0

Table 5.6 Interspecific regression analyses on data presented in Table 5.6
(32 degrees of freedom in all tests)

Independent variable	Dependent variable	Linear equation	r	p
Body length	Actual distance	$y = 117.14 \pm 17.77x + 220.21$	0.7589	***
Body length	Mean velocity	$y = 7.45 \pm 1.32x + 48.27$	0.7064	***
Body length	No. active mins.	$y = 0.33 \pm 0.07x + 7.36$	0.6165	*
Body length	Linear distance	$y = 23.64 \pm 9.76x + 179.73$	0.4161	**
Body length	Mean deviation	$y = -0.02 \pm 0.97x + 65.81$	-0.0031	NS
Mean deviation	Actual distance	$y = -1.75 \pm 4.97x + 1190.84$	0.0622	NS
Mean deviation	Linear distance	$y = -0.94 \pm 1.92x + 426.55$	-0.0861	NS
Mean deviation	Mean velocity	$y = -0.09 \pm 0.34x + 108.60$	-0.0469	NS
Mean deviation	No. mins active	$y = -0.01 \pm 0.01x + 10.11$	-0.0540	NS
Mean deviation	Linear:Actual distance ratio	$y = 0.00 \pm 0.00x + 0.45$	-0.1591	NS
Actual distance	Linear distance	$y = 0.21 \pm 0.06x + 143.27$	0.5327	**
Mean velocity	Linear distance	$y = 3.16 \pm 0.83x + 39.88$	0.5592	***

For units of variables see Table 5.5 (mean deviation = mean directional change/move)

* = 0.05 > P > 0.01 ** = 0.01 > P > 0.001 *** = P < 0.001 NS = not significant (p > 0.05)

Table 5.7 Intraspecific regression analysis: biotic independent

SPECIES	Indep. Var.	D E P E N D E N T						V A R I A B L E S					
		Actual Distance		Mean Velocity		Linear Distance		MD		MA			
		r	df p	r	df p	r	df p	r	df p	r	df p		
N. bigutt.	BS	0.4433	7 NS	0.4945	7 NS	-0.0944	7 NS	-0.4615	7 NS	0.3435	7 NS		
P. melan.	BS	-0.0546	7 NS	-0.0172	7 NS	-0.1026	7 NS	0.1193	7 NS	-0.2770	7 NS		
B. quad.	BS	0.6131	4 NS	0.7673	4 NS	0.3319	4 NS	0.3732	4 NS	0.1980	4 NS		
B. lamp.	BS	0.2416	4 NS	0.6129	4 NS	0.1282	4 NS	0.3817	4 NS	-0.6817	4 NS		
A. muell.	BS	-0.1341	2 NS	-0.0561	2 NS	0.1269	2 NS	0.3798	2 NS	-0.1230	2 NS		
N. bigutt.	MD	-0.6548	7 NS	-0.6171	7 NS	-0.3820	7 NS			-0.6958	7 *		
P. melan.	MD	-0.4476	7 NS	-0.4594	7 NS	-0.4561	7 NS			-0.1493	7 NS		
B. quad.	MD	0.9139	4 *	0.4119	4 NS	0.3988	4 NS			0.7871	4 NS		
B. lamp.	MD	0.6107	4 NS	0.6819	4 NS	-0.2471	4 NS			-0.0557	4 NS		
A. muell.	MD	-0.5593	2 NS	-0.8770	2 NS	-0.0534	2 NS			-0.1678	2 NS		
N. bigutt.	MA	0.8992	7 ***	0.7946	7 *	0.6188	7 NS			-0.6958	7 *		
P. melan.	MA	0.6155	7 NS	0.3463	7 NS	0.0288	7 NS			-0.1492	7 NS		
B. quad.	MA	0.7823	4 NS	-0.0412	4 NS	-0.2475	4 NS			0.7871	4 NS		
B. lamp.	MA	0.3437	4 NS	-0.1961	4 NS	0.3598	4 NS			-0.0557	4 NS		
A. muell.	MA	0.8996	2 NS	0.4975	2 NS	0.9684	2 *			-0.1678	2 NS		

* = 0.01 < p < 0.05 *** = p < 0.001 NS = not significant (p > 0.05)

BS=body size MD=Mean deviation/move MA=no. minutes active (for units of variables see Table 5.5)

Table 5.8 Intraspecific regression analysis (abiotic independent)

SPECIES	Indep. Variable	D E P E N D E N T				V A R I A B L E S				No. mins Active	
		Actual Distance		Mean Velocity		Linear Distance		Mean devn. /move			
		r	df p	r	df p	r	df p	r	df p	r	df p
N. bigutt.	TP	-0.0855	7 NS	-0.1687	7 NS	-0.2316	7 NS	0.0964	7 NS	0.3306	7 NS
B. quad.	TP	0.9711	4 **	0.6694	4 NS	0.3449	4 NS	0.6926	4 NS	0.8536	4 *
B. lamp.	TP	0.1986	4 NS	0.3993	4 NS	0.2245	4 NS	-0.2983	4 NS	-0.1028	4 NS

* = 0.01 < P < 0.05 ** = 0.001 < P < 0.01 NS = not significant (p > 0.05)

TP = temperature (for units of variables see Table 5.5)

Table 5.9 Comparison of initial and subsequent activity

Species	Mean distance moved in first minute (mm)	Mean subsequent distance moved (mm/minute)
<i>N. biguttatus</i>	103.88 ± 28.66 (n=9)	29.21 ± 3.93 (n=126)
<i>P. melanarius</i>	88.89 ± 14.45 (n=9)	132.42 ± 10.18 (n=126)
<i>B. quadrimaculatum</i>	49.17 ± 14.16 (n=6)	40.18 ± 6.06 (n=84)
<i>B. lampros</i>	75.83 ± 27.01 (n=6)	63.39 ± 6.94 (n=84)
<i>A. muelleri</i>	130.00 ± 33.42 (n=4)	80.36 ± 11.94 (n=56)

Results of Mann Whitney U test

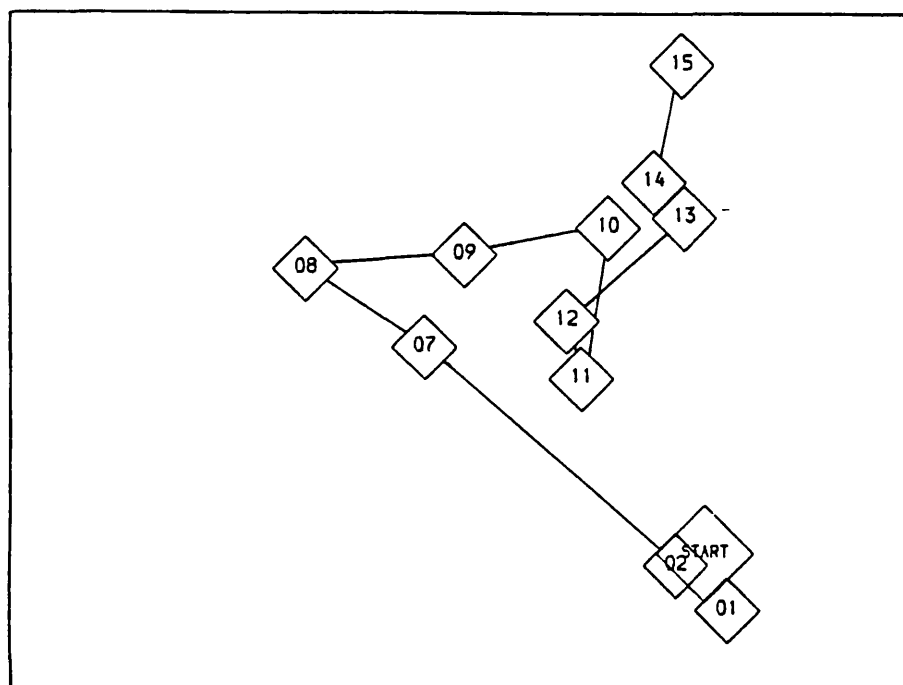
Species	$\sum R_i$	U	z_U	p
<i>N. biguttatus</i>	209.5	969.5	3.5504	***
<i>P. melanarius</i>	701.5	477.5	-0.7895	N. S.
<i>B. quadrimaculatum</i>	197.5	327.5	1.2210	N. S.
<i>B. lampros</i>	238.0	287.0	0.5661	N. S.
<i>A. muelleri</i>	71.0	163.0	1.5114	N. S.

p = probability that the null hypothesis is false.

*** = $p < 0.001$ N. S. = not significant ($p > 0.05$).

For explanation of symbols used see Appendix 7.

Fig. 5.1 Diagrammatic representation of movement in the field

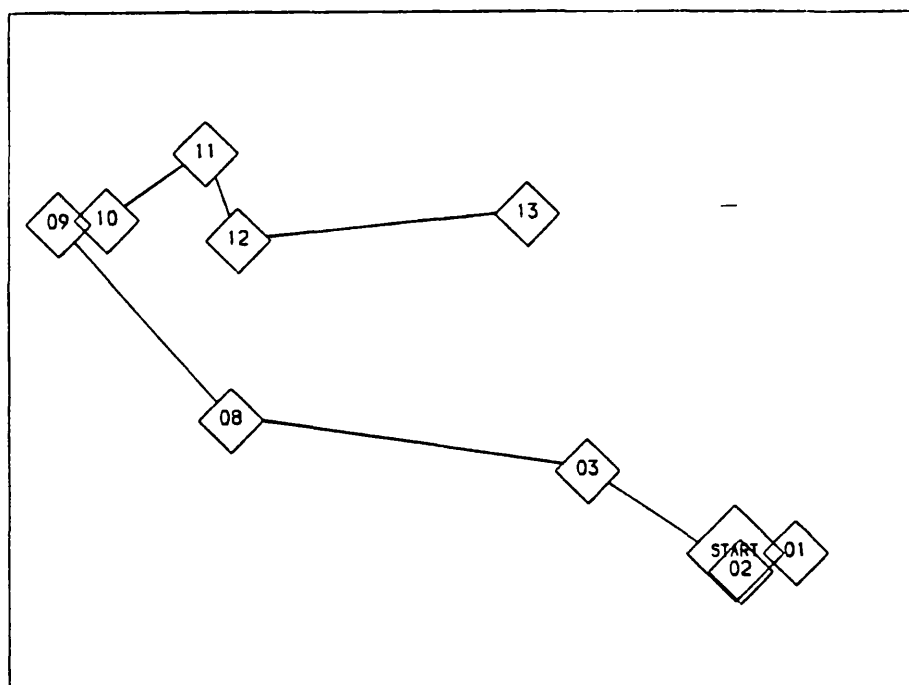


Bembidion lampros Ref. A97.

Scale: 100mm

Centre of each figure refers to position of beetle.
Numbers refer to the time from the start (in minutes)
of the first observation of each position.

Fig. 5.2 Diagrammatic representation of movement in the field

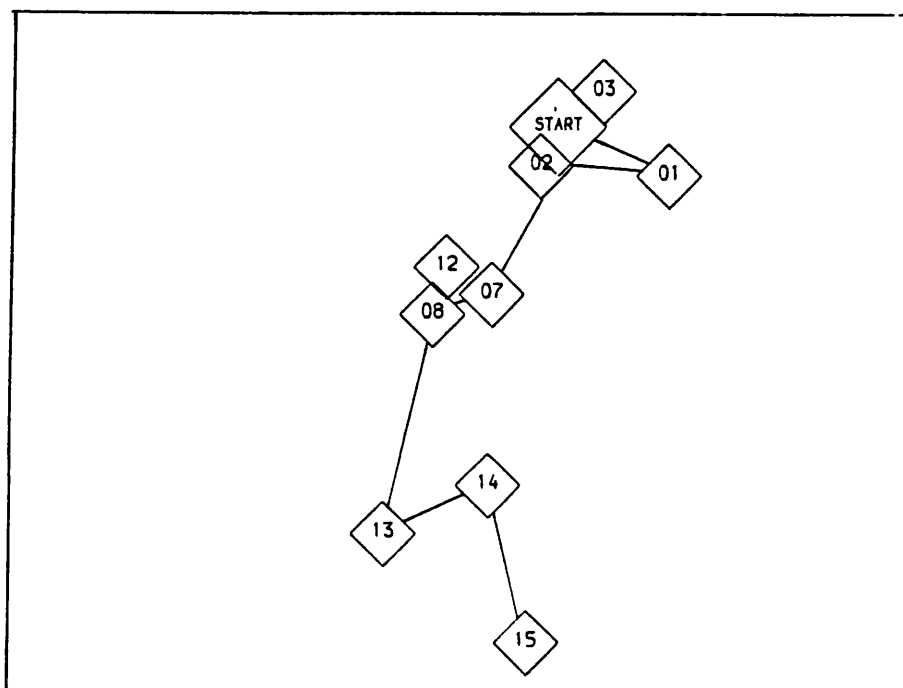


Agonum muelleri Ref. A03.

Scale: 150mm

Centre of each figure refers to position of beetle.
Numbers refer to the time from the start (in minutes)
of the first observation of each position.

Fig. 5.3 Diagrammatic representation of movement in the field



Agonum muelleri Ref. A09.

Scale: 150mm

Centre of each figure refers to position of beetle.
Numbers refer to the time from the start (in minutes)
of the first observation of each position.

Fig. 5.4 Frequency distribution of distance moved between observations at 1 minute intervals

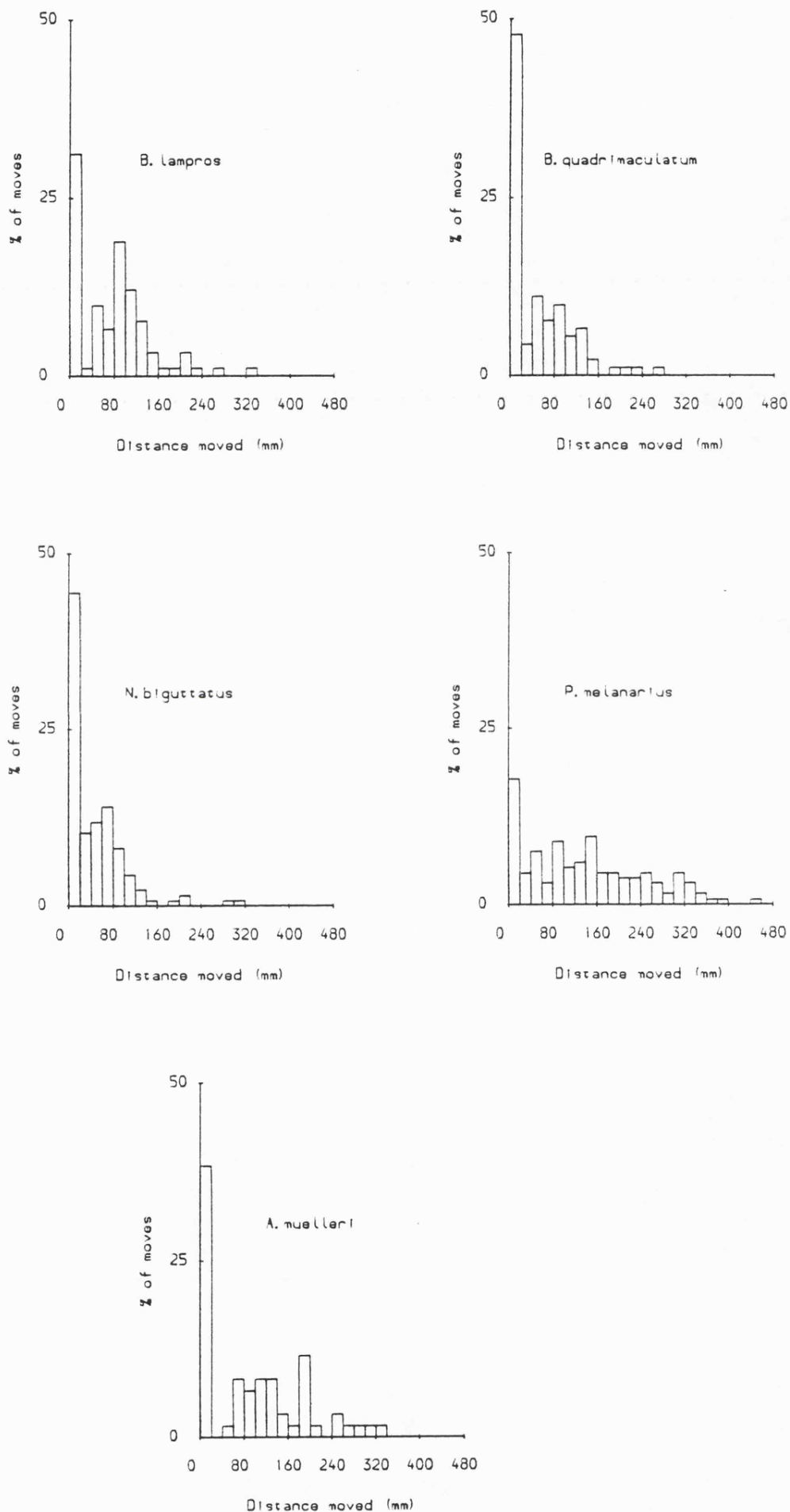
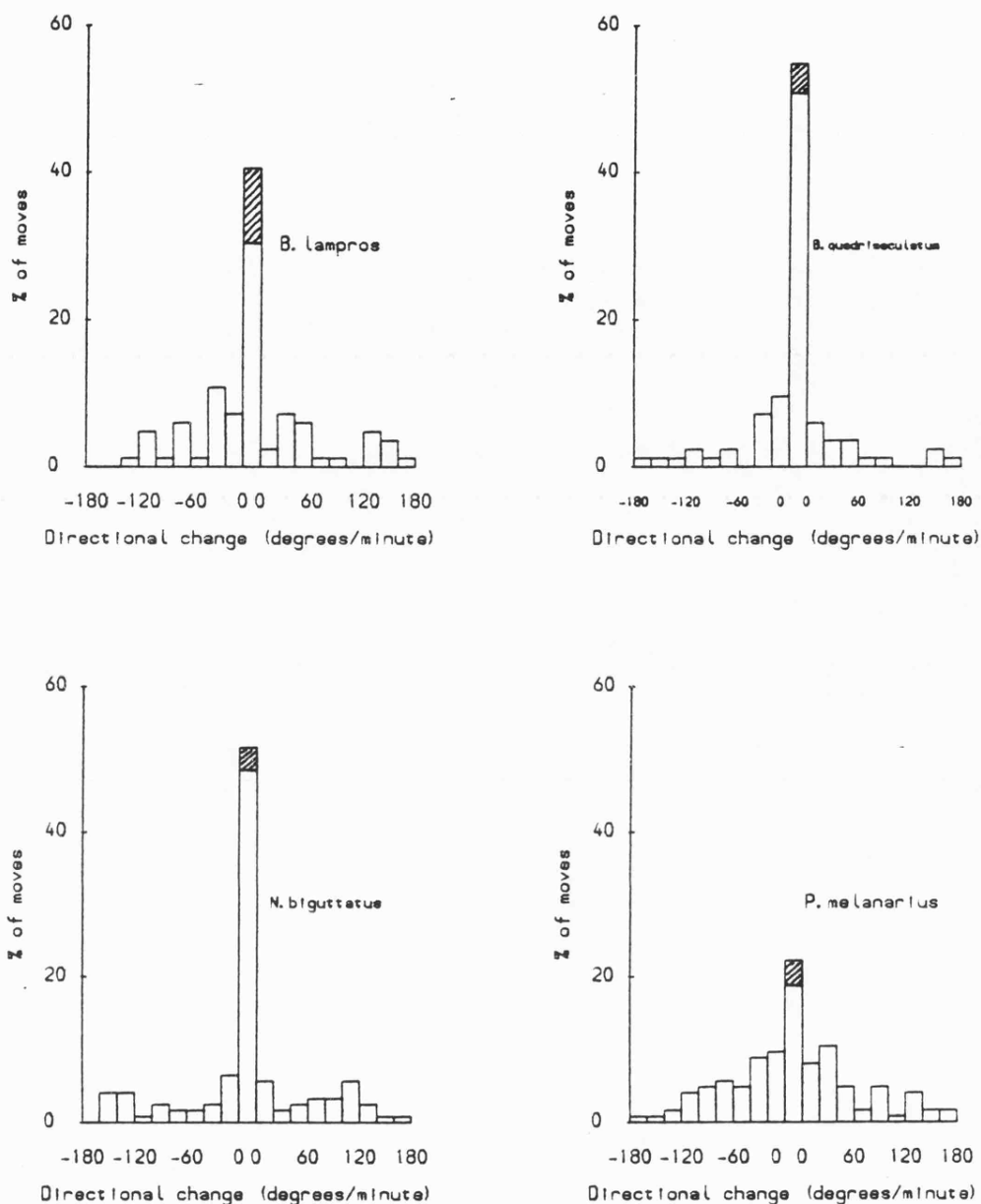


Fig. 5.5 Frequency distribution of changes in direction between observations at 1 minute intervals



Hatched areas of bars represent the percentage of minutes in which movement occurred but no change in direction was observed,

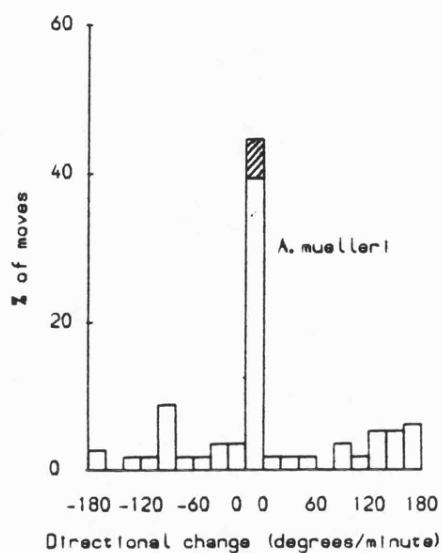


Fig. 5.6

Relationship between actual distance
moved and individual body length

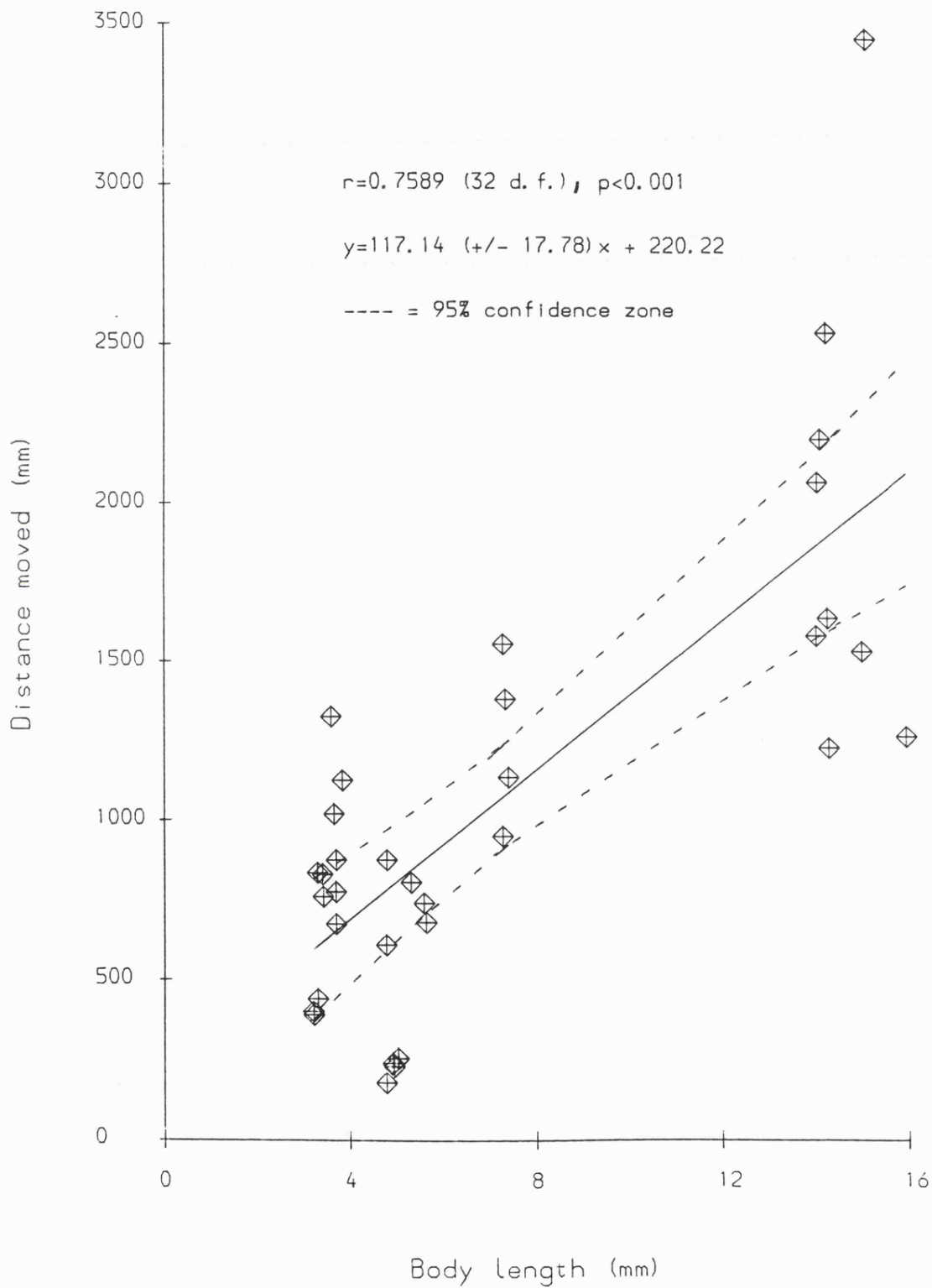


Fig. 5.7

Relationship between linear distance
and individual body length

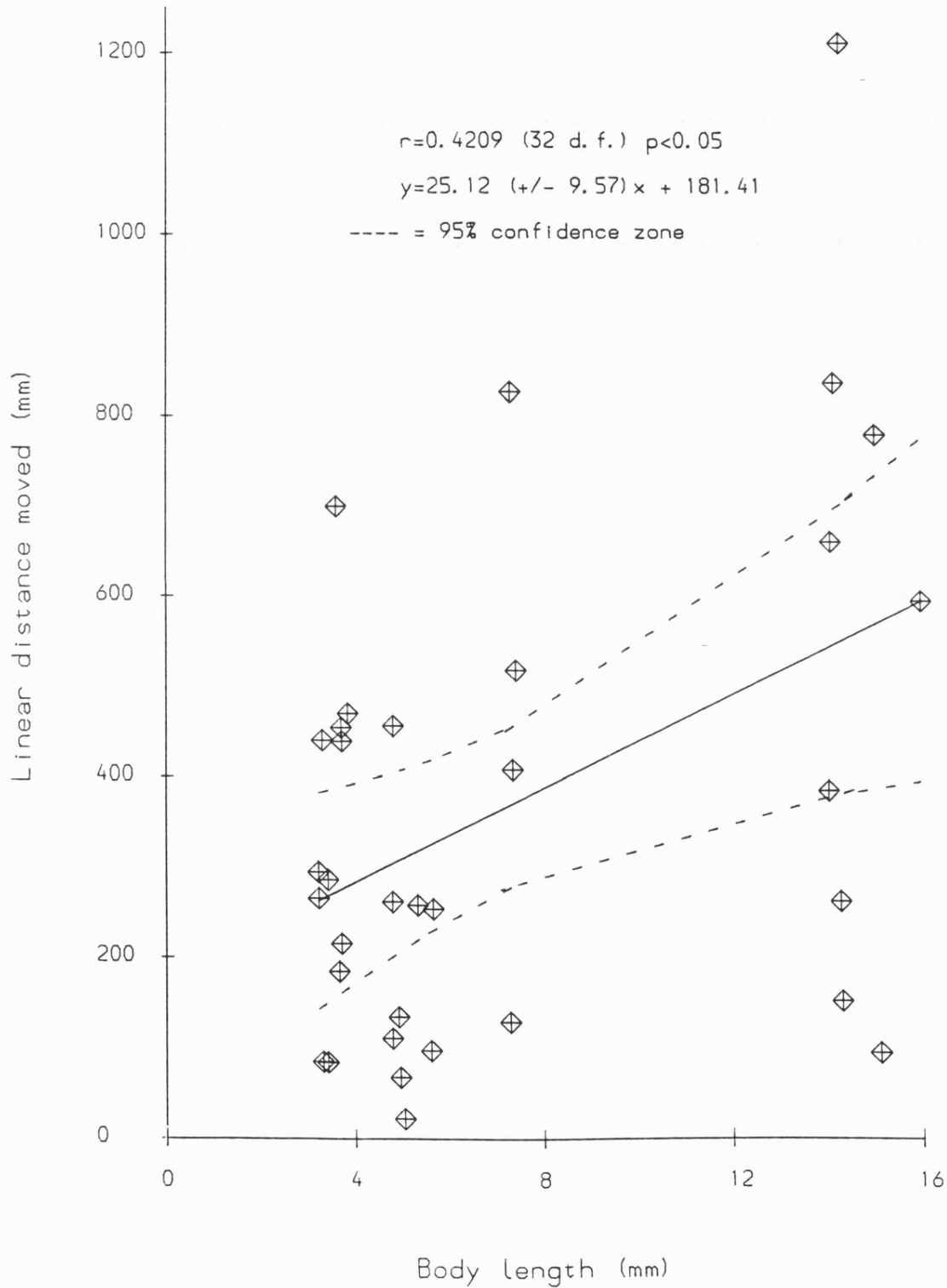


Fig. 5.8

Relationship between proportion of time spent active and individual body length

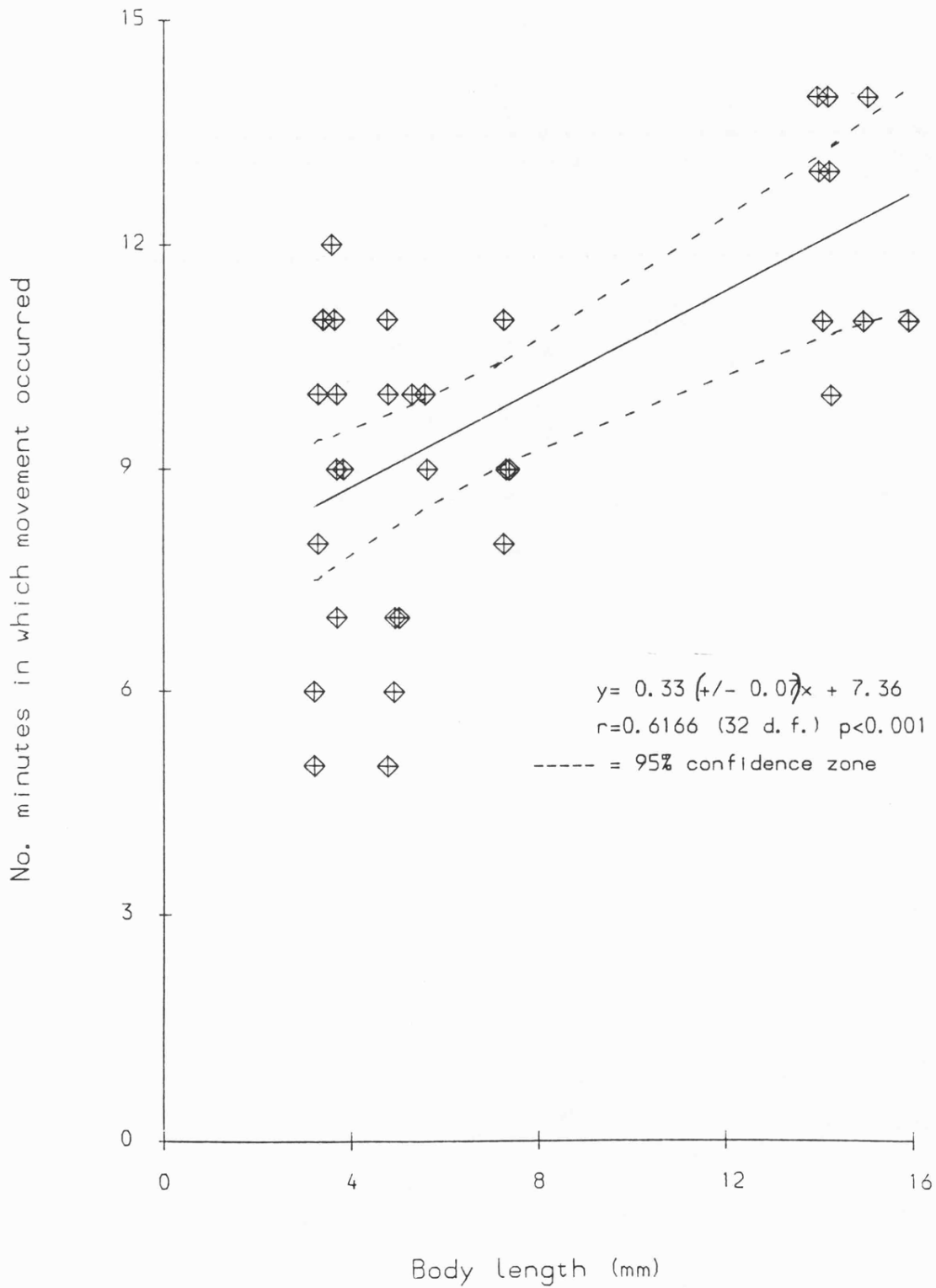


Fig. 5.9

Relationship between mean velocity
and individual body length

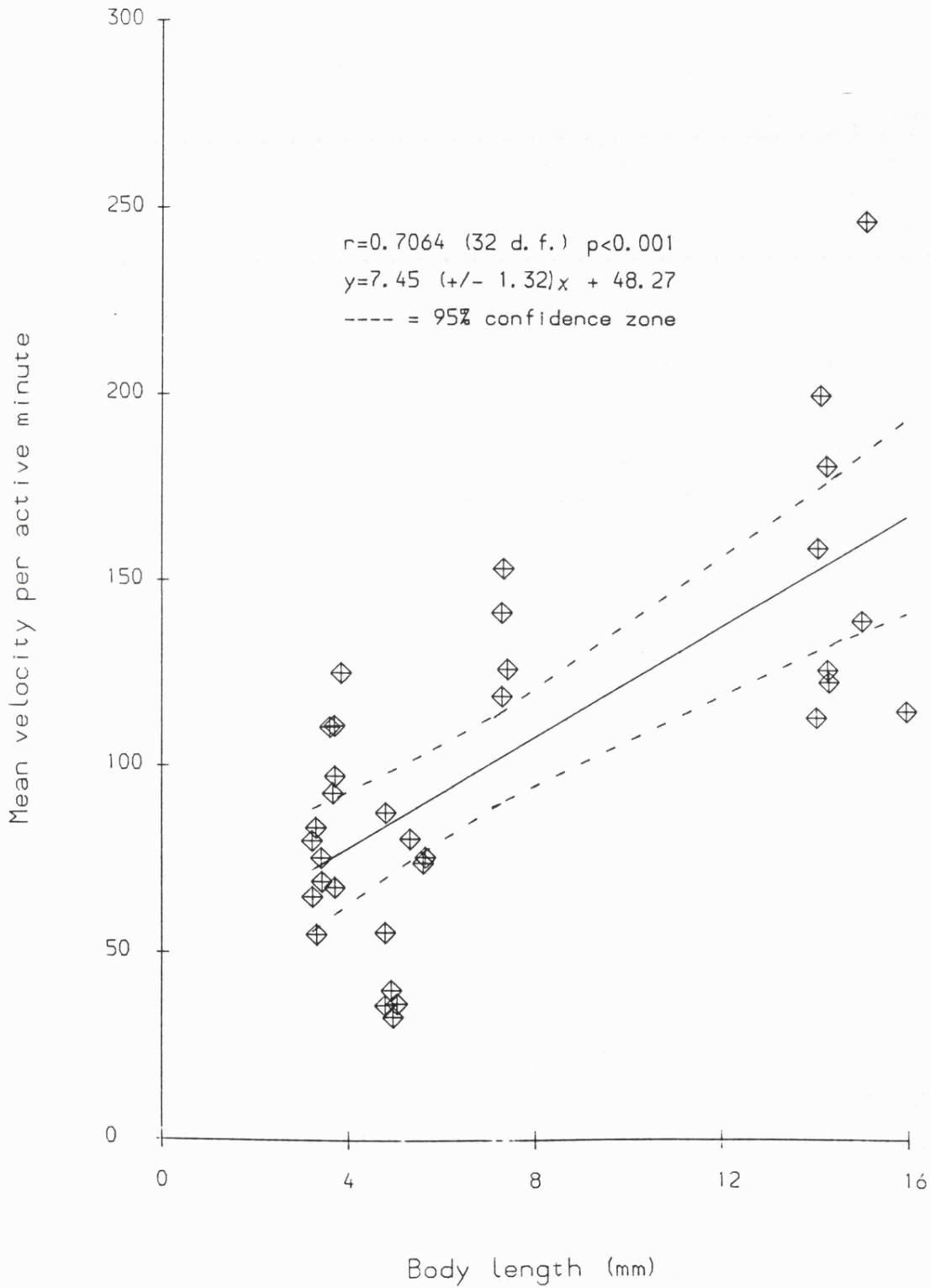
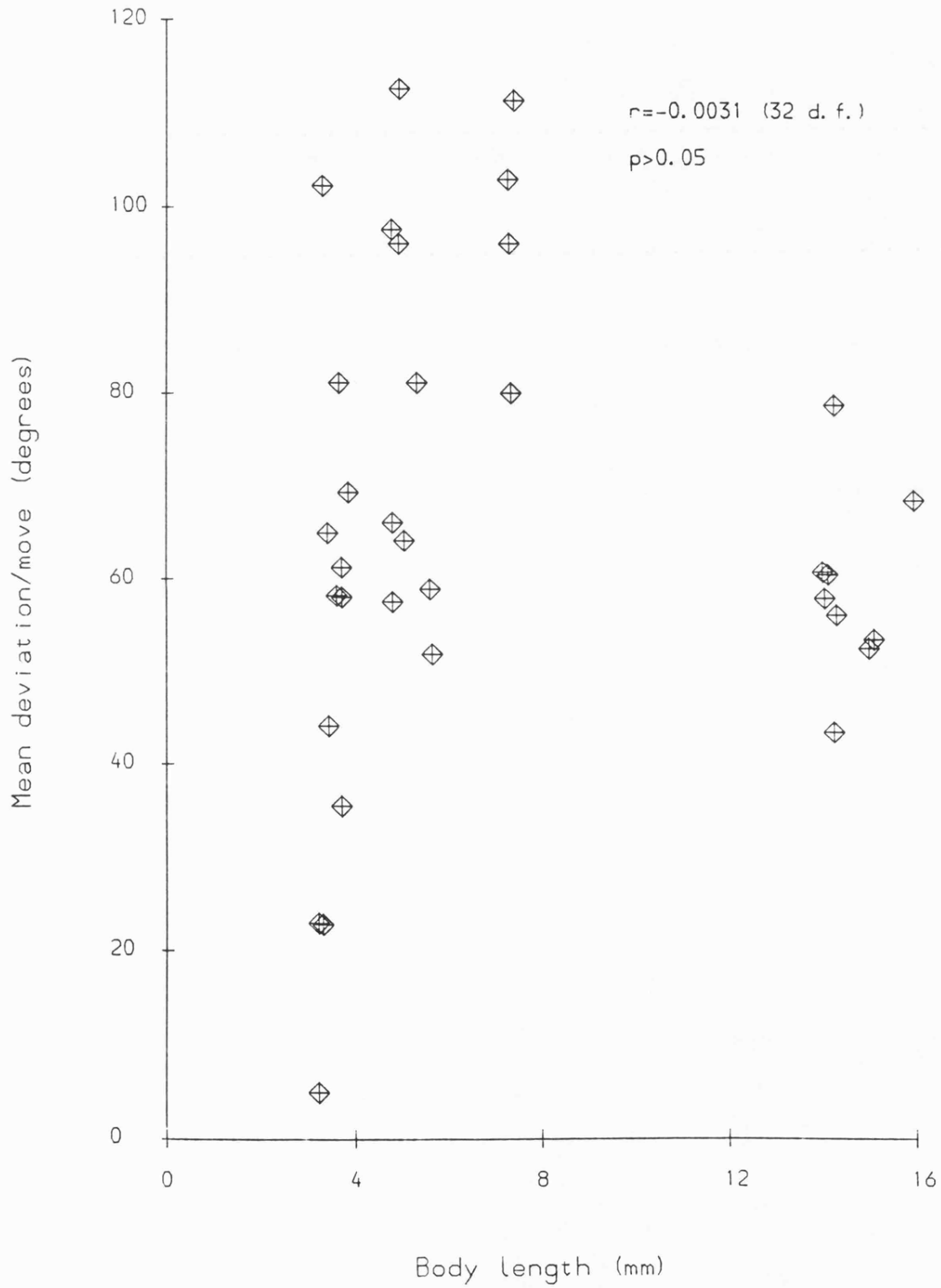


Fig. 5.10

Relationship between mean deviation
and individual body length



5.4 Discussion

The monitoring technique employed in the present study involved the close proximity of the observer to the beetles and the placement of pegs in the ground. Its validity is open to question because of the possible effects of interference by the observer.

Although the assumption, that the disturbance caused by the observer had no effect on the activity of the beetles, was not tested (no statistical test on the data is possible), subjective observations in the field lead me to believe that the beetles reacted very little to my presence or to the placement of pegs in the ground (this was done after the beetle had moved from its position). Beetles seemed to move towards as often as away from me.

Hasselmann (1962) reports that carabid beetles are insensitive to far red light ($\lambda > 675\text{nm}$) but the red light used in the present study transmitted visible light at a lower frequency. It is possible that individuals of *P.melanarius* responded to this with increased locomotor activity.

One statistical test is possible - to test the hypothesis that the activity of beetles in the first minute after release is not significantly different from the mean subsequent activity. Beetles were confined for up to 20 minutes prior to release and it was necessary to handle them to some extent. It might be expected that if beetles were to show effects of disturbance in the form of increased activity then this would be most apparent upon release from confinement. The null hypothesis was found to be true for four out of the five species studied (Table 5.9). This statistical test does not discount the possibility that beetles demonstrated increased activity for the whole period of observation but the fact that beetles often remained stationary for several consecutive minutes supports the

hypothesis of no disturbance and leads one to believe that the patterns of movement recorded in the field are realistic. Further, the very variable behaviour patterns, as indicated by the high standard errors, suggest a lack of uniform 'alarm' response.

Other methods of monitoring activity, such as the use of radioactive tracers (Baars, 1979b) or biological tags (Meijer, 1975) do not allow beetles to be monitored continually. The possible disadvantages of the technique employed here have to be weighed against the advantages of being able to continuously monitor activity and these are considerable.

Thiele (1977) reviews locomotor activity in the Carabidae and it seems that other close observations of patterns of movement in the field have not been published. According to Thiele (1977) Heydemann (1957) made observations on velocity in different habitats but a copy of the paper could not be obtained.

Brunsting (1983) used radioactive phosphorous paint in the laboratory so that beetles could be monitored both visually and with an event recorder (an adapted Geiger-counter). He warns of the possible effects of an unusually high density of individuals in his experiments (12 to 24 m^{-2} although he justifies his results by stating that very few interactions between beetles occurred in over 30 hours observation. Even so, it is possible that beetles reacted to the presence of other beetles in some way and their true activity patterns were not recorded. The beetles were also fed *ad lib.* and were therefore in an unrepresentative physiological state. Grüm (1971) has shown that locomotor activity is increased when satiated beetles are deprived of food.

It has been argued in this chapter that estimates of actual distance traversed are unreliable unless the time interval between

observations is small. The use of pitfall traps to estimate actual distance is not a satisfactory technique - they can only be used to estimate the linear distance traversed between observations (captures).

Because the distances moved by carabids quoted by other authors are the shortest distance between two observations separated by many hours, they are not really comparable with data on the actual distance moved in the present study. The actual distance travelled by a beetle will always be greater than or equal to the linear distance between two consecutive observations of its position.

Extrapolation from the results of Thiele (1977) for *P.melanarius* (8.1cm/second) gives an actual distance of 72.9m in 15 minutes! This is clearly an overestimate of actual distance since Thiele observed continually moving beetles and data from the present investigation suggest that beetles spend 18 - 48% of whole minutes stationary.

Only Brunsting (1983) gives comparable data for actual distance travelled by *P.oblongopunctatus* which incorporates stationary periods (see p.163). Extrapolation of his laboratory results (given in m/hr) gives a distance which is approximately 1/3 of the predicted actual distance for this species from the regression of actual distance on body length. In other words, individuals of *P. oblongopunctatus* did not travel as far as expected from the hypothesis. The fact that beetles were studied in the laboratory and at high densities may partly account for this (but see also p.163).

The linear distance between the first and last observations in the present study (separated by 15 minutes) are perhaps comparable with other studies, although at 15 minutes the time interval is still much shorter and considerable extrapolation is necessary. Comparisons based on extrapolation of one set of data are open to question

(Thiele, 1977) but are sometimes useful. The predicted linear distances for the two species studied by Baars (1979b) were 2 to 5 times greater than he observed for *Pterostichus versicolor* and *Calathus melanocephalus* respectively (see p.161). This difference is to be expected since the ratio of the number of observations in the two studies is 1:96 (every 24 hours and every 15 minutes). In both studies, the indication is that linear distance and body length are correlated.

Baars (1979a) found that the linear distance travelled between observations was related to temperature in *Calathus melanocephalus* but regression analysis was not possible due to the high variability of the dependent variable at high temperatures. Vlijm et al. (1961) also found temperature to be proportional to locomotor activity in the field in *Calathus* spp. although activity was not studied in great detail. No relationship was found between the two variables in the present study when intraspecific data were analysed. It should be pointed out that this was not one of the main objectives of the study and so the range of the independent variable is narrow.

The mean velocity for *P.oblongopunctatus* presented by Brunsting (1983) includes stationary periods of up to 30 seconds (see p.163). In the present study stationary periods of up to 120 seconds were incorporated in the estimate of mean velocity. To determine velocity accurately in the field it would be necessary to use a video camera and a coordinate grid so that monitoring is truly continuous and quantifiable. However, this would perhaps defeat one of the objectives of such a study - to estimate velocity under natural conditions with minimum disturbance.

Close agreement between the predicted mean velocity and that observed by Brunsting (1983) further supports the hypothesis that

velocity is dependent upon body length in the Carabidae. Clearly this relationship will only hold for beetles of a similar body form (Forsythe, 1987b) such as those discussed in this chapter.

Some of the findings of Heydemann (1957) are reported by Thiele (1977) and of particular interest are the data on the two *Carabus* species. *Carabus auratus* (body length = 23.5mm [Lindroth, 1974]) had a mean velocity (continual monitoring) of 1.8 to 2.3 m min⁻¹ in arable fields. Similarly, *C.cancellatus*, which has the same body length, had a mean velocity of 1.7 m min⁻¹ in winter cereal. The predicted mean velocity for both species from the present study is 0.223 ± 0.029 m min⁻¹. The *Carabus* genus belongs to what Forsythe (1987b) classes as Carabinae Group I (there are 3 groups which relate structural differences to locomotor activity) and are faster runners than other carabids. Hence the values might be expected to be higher since the regression is based on Carabinae Group II species.

This structural difference alone cannot explain the 9:1 and 7.6:1 ratio of the two actual:predicted estimates of velocity. Further explanation lies in the fact that the present study underestimates velocity because the proportion of time spent stationary between observations were not recorded. For the estimates to be comparable, these beetles would have to spend approximately 88% of their time stationary. Subjective observations of beetles in the field reveal that locomotor activity is characterized by short bursts of movement separated by stationary periods and this is supported by quantified observations of locomotor activity of *N. biguttatus* in the laboratory (see Chapter 4). *N. biguttatus* is renowned for its unusual pattern of movement which, it is thought, is an adaptation to predation on Collembola (Bauer, 1982). However, Brunsting (1983) reported that the stationary periods also account for up to 2/3 of the time devoted to locomotor activity in *P.oblongopunctatus* in the

laboratory, thus giving quantitative support to the hypothesis that the pattern of locomotion is common to carabids of a similar body form i.e. members of Carabinae groups I and II (Forsythe, 1987b).

When the mean number of minutes positive for movement are compared interspecifically then significant differences are found between *P.melanarius* and all three species characterized by smaller sized individuals. The parameter is significantly correlated with body length. It can therefore tentatively be suggested that larger beetles are more active than smaller ones. Unfortunately, no interspecific comparisons occur in the literature to support or disprove this finding.

Brunsting (1983) found that less than 10% of individuals of *P.oblongopunctatus* were active at any one time. This is a much lower estimate of the proportion of time spent active than would be predicted, for a beetle of this size, from the regression in the present study. It is possible that this value is more realistic for the species studied here because the accuracy of the parameter 'proportion of time spent active' is determined by the time between observations and is likely to overestimate the true value.

The only data published on directional changes within such small time intervals for the Carabidae is that of Brunsting (1983) in the laboratory. For every 3cm moved by individual beetles, the bearing was recorded and the difference between consecutive bearings used to calculate the directional deviation. Siniff & Jessen (1969) point out the difficulties in relating deviation to other parameters and such a difficulty was encountered here too. The parameter could not be related to any other in the present study making it impossible to relate the pattern of movement of beetles to their body size.

Species-specific differences with respect to mean deviation were found in some cases, but the factor determining this difference could not be ascertained.

Patterns of movement and body length

Although linear distance and actual distance are related variables, and both are significantly correlated with individual body size, no overall relationship between the pattern of movement and individual body size could be found. This is because the angle of deviation is independent of body size. The patterns of movement do clearly differ in many respects, and one way to quantify this is to use some form of census of simulated movement. The chance of a moving individual encountering a pitfall trap is the most obvious form of census.

Baars (1979b) found agreement between actual pitfall captures and simulations of his field observations of day-distances and day-directions. In the laboratory, Brunsting (1983) made more detailed observations of locomotor activity and he found a similar relationship. The best features of both these approaches were incorporated in the present study: detailed observations were made in the field and the data from field observations were simulated on a computer (Chapter 6).

CHAPTER 6

Simulation

6.1 Introduction

The data on activity collected from the field can be used to simulate beetle movement within a theoretical coordinate grid of pitfall traps in the memory of a computer. The aim of simulating beetle movement is to calculate, for several species, an individual's probability of encountering one of the pitfall traps in the grid. This probability is calculated at several different durations of movement. Once this value has been obtained, an estimate of the number of beetles which would have been captured if interspecific differences in activity and avoidance were accounted for can be calculated. This is achieved for each species by modifying actual pitfall data using the two parameters: probability of encountering a trap and rate of avoidance following an encounter.

When these parameters are taken into account, the estimated number of individuals of each species captured should more closely resemble their absolute density (as determined in Chapter 3) than do pitfall-trap captures from the field.

The interspecific differences in avoidance rate which were revealed in Chapter 4 emphasise the importance of incorporating this parameter in any modification of pitfall-trap data. Since the avoidance rate for each species is known, an estimate of the number of individuals which actually encountered traps in the field can be calculated from pitfall-trap data for each species. For example, for every individual of *Notiophilus biguttatus* (86.7% avoidance) captured it may be inferred that there were 7.52 encounters (or more practically, for every 13 captures there were

approximately 100 encounters. This can be represented for each species by a simple equation:

$$\hat{N}_{enc} = N_{cap} / [1-A] \quad (1)$$

where $\hat{N}_{enc}$ = estimated number of individuals which encountered traps in the field

N_{cap} = actual number of individuals captured by traps in the field

A = proportion of encounters resulting in avoidance
(experimentally determined)

For species with relatively high avoidance rates, such as *B. lampros* and *N. biguttatus*, the difference between $\hat{N}_{enc}$ and N_{cap} will be greater than for species with relatively low avoidance rates such as *Pterostichus melanarius*.

The probability of an individual encountering a trap can be determined by simulation of movement patterns of individual beetles. The activity data presented in Chapter 5 may be used for this purpose. If individuals of a group of several species are released onto the hypothetical grid of pitfall traps for a fixed period of time and move according to these data then the proportion of individuals of each species encountering traps at the end of such a period can be calculated:

$$P_{enc} = N_{enc} / N_{rel} \quad (2)$$

where P_{enc} = proportion of individuals encountering traps in simulation

(=probability of one individual encountering traps)

N_{enc} = number of individuals encountering traps in simulation

N_{rel} = number of individuals released

The parameter P_{enc} can be taken as being equivalent to the probability of any one individual of the species encountering a trap in the hypothetical grid, hereinafter referred to as $\hat{P}_{enc}$ since it is effectively an estimate of the probability of an individual encountering a trap in a similar grid in the field. Species with relatively low mean velocities such as *B. lampros* and *N. biguttatus* will have a relatively low probability of encountering traps and the difference between N_{enc} and N_{real} will be great relative to species with a relatively high mean velocity such as *P. melanarius*.

It will become apparent later that to simply equate $\hat{P}_{enc}$ (equation 2) to N_{enc} (equation 1) to allow the determination of the total number of individuals in the population is an unsatisfactory approach to the problem of prediction of population density. To do this accurately, it is necessary to estimate another parameter.

Once the probability or proportion, $\hat{P}_{enc}$, is estimated then the following equation can be computed for each species:

$$\hat{N}_{cap} = N_{cap} * (1 / (1 - A * \hat{P}_{enc})) \quad (3)$$

where $\hat{N}_{cap}$ = estimated number of individuals trapped

N_{cap} = actual number of individuals trapped in the field

$\hat{P}_{enc}$ = estimated probability of an individual encountering a trap in the field

A = proportion of encounters resulting in avoidance

For this equation to be satisfied, the duration for which activity is simulated on the hypothetical grid should be equivalent to the duration for which traps were operative in the field in order to collect data for the

variable N_{cap} . This is because P_{enc} (from simulation) is equivalent to the field estimate $\hat{P}_{enc}$, which in turn determines N_{cap} .

Equation 3 estimates the number of individuals captured corrected for interspecific differences in avoidance rate and probability of encounter. It produces a hypothetical value, $\hat{N}_{cap}$, which is effectively the number of individuals which would have been captured if no interspecific differences with respect to these parameters existed.

The two parameters A and $\hat{P}_{enc}$ are denominators in the equation since species with high avoidance rates and low probability of encountering traps are underrepresented in pitfall traps in the field when compared with other species. N_{cap} needs to be increased to compensate for this and for these species $[1-A]$ and $\hat{P}_{enc}$, as relatively small denominators, will increase N_{cap} accordingly. Conversely, species with low avoidance rates which have a relatively high mean velocity can be overrepresented in traps relative to other species and N_{cap} for these species will be increased proportionally less so that the ratio $\hat{N}_{cap}:N_{cap}$ is smaller.

The estimated relative abundance of each species in pitfall traps, corrected for interspecific differences in avoidance and encounter rates, is given by:

$$\hat{P}_{icap} = \hat{N}_{icap} / \sum_{i=1}^s \hat{N}_{icap} \quad (4)$$

where $\hat{P}_{icap}$ = the estimated corrected relative abundance of species 1 in pitfall traps

$\hat{N}_{icap}$ = the estimated corrected number of individuals of species 1 captured

s = the number of species

It has been shown by many workers (e.g. Briggs, 1961; Lesiewicz *et al.*, 1983) and by analysis of data presented in Chapter 3 of the present study (see Tables 6.4 and 6.5) that the relative abundance of species in pitfalls in the field (P_{cap}) bears little relation to relative population density in the vicinity of the traps (as determined by quadrats and mark-release-recapture). This is because pitfall traps selectively capture species with relatively high mean velocities and low avoidance rates and hence these parameters which differ interspecifically are not accounted for when comparisons are made between the two types of relative abundance across a group of species.

In this thesis it is postulated that there should be a more significant interspecific correlation between $\tilde{P}_{cap}$ (equation 4) and relative abundance in the field than between P_{cap} and relative abundance in the field. This is because the above equation (3) takes into account species specific activity patterns and avoidance rates, so that the estimated number of individuals of a species captured ($\tilde{N}_{cap}$) is adjusted so as to be in proportion to the species' absolute abundance. This hypothesis may be tested by statistically comparing both $\tilde{P}_{cap}$ and P_{cap} with relative abundance estimates interspecifically on several different occasions for which data on absolute abundance and pitfall trap captures are available.

If this proves successful, relative abundance of a group of species could be predicted from the parameters N_{cap} , P_{enc} and A alone. It should then only be necessary to know the absolute abundance (in terms of the number of individuals m^{-2}) of one of these species to determine the absolute abundance of all the other species in the group being considered.

6.2 Simulation program

6.2.1 Movement

A FORTRAN program (Appendix 4) was developed during the

course of this study which simulated beetle movement on a coordinate grid containing 'traps' at intervals equivalent to the distances between traps in the field. Kitching (1971) constructed a similar grid using FORTRAN in order to simulate animal movement patterns but with a number of different habitats scattered within it.

The traps defined in simulations were of the same diameter at the soil surface as were the small pitfall traps used in the field i. e. 5.5cm. The grid was much larger (5000m square) for reasons discussed later and contained over 1 million traps.

The movement patterns of individuals of the 5 species studied in Chapter 5 were simulated by using the actual field data for individuals of these species (i. e. the distance travelled per minute and the angular deviation per minute). Consecutive positions of beetles were calculated as described in Chapter 5 (p.159).

Beetles were 'released' individually at a mid point between four traps in the centre of the grid and their movement determined by a mathematical formula into which field data on activity (velocity and angular deviation) were input. The distance moved each minute and the bearing of the position of the beetle from its previous position were known and were contained in a data file accessed by the main program. Hence the following lines extracted from the program (modified here for simplicity) move the beetle to its new position and determine whether or not it has been captured.

<u>FORTTRAN</u>	<u>Explanation</u>
2 H=H+A X=X+SIN(A)*D Y=Y+COS(A)*D XN=ANINT(X) YN=ANINT(Y) DX=ABS(X-XN) DY=ABS(Y-YN) DXY=SQRT(DX**2+DY**2) IF (DXY.LE. R) THEN T=1 GOTO 3 ELSE T=0	Coordinates determined All trap coordinates made equivalent Check for critical coordinates i. e. has the beetle encountered a trap?

```
GOTO 2
ENDIF
3 CONTINUE
```

X and Y are the coordinates which define the position of the beetle on the grid.

A = angle of deviation from previous direction - new data each move

D = distance moved since previous position - new data each move

R = the radius of the trap

T = whether a beetle has been trapped (1) or not (0)

ANINT = nearest whole number: $\text{REAL}(\text{INT}(V + 0.5))$ or $\text{REAL}(\text{INT}(V - 0.5))$

ABS = absolute value: $[\text{REAL}(V)^2]^{1/2}$

where V = X or Y coordinate

A beetle will continue to move about the grid according to the data collected from the field until it is trapped (in the simplified extract above, a 0% avoidance rate is assumed). This will occur if the coordinates of the beetle correspond to the coordinates of one of the traps. These coordinates are checked after each move. In the grid the area occupied by each trap is defined by unique coordinates. However, the extract from the program shows how all trap coordinates are made equivalent so that only one conditional IF statement needs to be computed. The area occupied by this single trap can be defined in terms of its radius alone using the FORTRAN functions ANINT and ABS on the coordinates which define the position of a beetle after each move.

A counter placed later in the program allows the number of beetles trapped to be monitored. The final value, on completion of the simulation, is written to a data file.

6.2.2 Duration

In the full version of the program, further lines were included to limit the time a beetle could spend on the grid. These times ranged from 2 to 16 days. This was achieved by effectively repeating the above loop the required number of times, each repeat representing one minute's activity. It was assumed that beetles were active for 12 hours

each day and so for every 24-hour period spent on the grid, the 15 minute data sets were repeated 48 times.

The 15 minute data sets were used as many times as necessary according to the number of individuals released. For example, 9 individual 15 minute data sets were available for *N. biguttatus* and *P. melanarius*. 1008 individuals of each species were 'released' on the grid and so the data sets were used 112 times each.

Each time an individual beetle was released on the grid a different starting angle was used for the first move (this was determined by the FORTRAN random number generator RAN and the parameter ISEED). This random angle becomes A in the simplified program extract presented above, and all future bearings are dependant upon it since the actual deviation between moves as recorded in the data file is added to the current bearing. Only 15 minutes of data were available for each individual released and so each 15 minute data set was repeated according to the total number of minutes spent on the grid. Because only 15 minutes worth of data were available for each individual, on the 16th move (and on the 31st, 46th etc.) the data for the first move was reused.

Because no angular deviation was recorded for the very first move in the field, on these moves the mean angular deviation from the 15-minute data set was used as opposed to the random angle generated for the very first move for each individual.

If a beetle was captured before its maximum time had elapsed, then another beetle was released in its place for the remaining fraction of the release period. In this way population density could be kept constant and the species' probability of encountering traps not decreased. The conditions governing release of such individuals were the same as those presented above i.e. equidistant from the four central traps and with a randomly-generated starting angle.

The time between emptying pitfall traps in the field was known for each of these periods. Beetles could therefore be released on the grid for durations equivalent to these times and their probability of encountering traps obtained. A series of durations of activity other than these was also simulated in an attempt to find trends and relationships within the data.

6.2.3 Avoidance

The program extract presented above assumes a 0% avoidance rate and so the number of individuals captured is equivalent to the number of individuals encountering traps. In the full version of the program however, the avoidance parameter was incorporated to make the simulation more realistic. A random number generator and a conditional IF statement were utilised so that at each encounter, the random number could be compared with the probability of a beetle avoiding a trap. If the random number was greater than the avoidance rate for the species then the beetle was trapped. If it was equal to or less than this value then the beetle avoided the trap. One possible inaccuracy in this respect is that avoiding beetles were relocated 0.5m from the trap but this was necessary to avoid multiple encounters with the trap in the loop outlined above (this would in turn give an artificially high estimate of β_{enc}).

No data was available to help decide what distance from traps beetles should be relocated; in reality, beetles tend to move away from traps and avoid multiple encounters but this was difficult to quantify and incorporate into the simulation. The distance chosen was to some extent an arbitrary one but an attempt was made to make it a compromise between the prevention of multiple encounters and relocating beetles at unrealistic distances from traps by referring to activity data from the field. The implications of this are discussed further in Section 6.4.

Beetles were also relocated if they reached the edge of the grid. The relocation point was the centre of the grid. The chance of this occurring

was minimised by initially releasing individuals in the centre of the very extensive grid and this precaution is only really necessary during particularly long simulations.

6.2.4 Density

The simulation program allows species to be released in different ratios of population densities. In the present study, however, the same number of individuals of each species was released. To ensure that the sum of this number and the duration of release did not vary interspecifically as simulations progressed, beetles which were trapped were replaced by other individuals i. e. population density was kept constant with respect to time. Replacing a trapped individual with another beetle did not result in an increase in the number of individuals released (N_{rel} - see equation 2 p.196) since the aim was to release a fixed number of individuals for the full duration.

It would be valid to release species in proportion to their actual abundance and compare the number captured in simulations with the number captured in pitfall traps in the field. The reason such an approach was not adopted in the present study was because the overall aim was to predict actual abundance, which is difficult to determine, from pitfall trap data, which is relatively easy to collect. It could be argued that the reverse approach is suitable for testing the theoretical equation (3) since data on absolute abundance are available but other problems are associated with its use (see Section 6.4). It seems sensible to use the predictive approach since this is the technique which will be most useful in the future.

6.2.5 Output

The final data file contains the following information on each line for each species studied:

1. the number of individuals released
2. the duration of the activity period in multiples of 12 hours
3. the number of encounters with traps
4. the number of beetles captured

A large number of beetles of each species could be released (although not simultaneously) and the proportion of individuals encountering traps determined for each species for different lengths of time the individuals of each species spend on the grid. The proportion of encounters resulting in avoidance during each species' simulation can also be calculated.

Simulations were performed on the five species for which both activity and avoidance data existed. However, the results of simulations on data from only four of these species could be used in a comparative way with data on population density (*Agonum muelleri* is the exception since its population density was not estimated). This species was included in simulations because of its intermediate body size thus allowing greater representation across variables in statistical analyses.

6.3 Results

Each move of a beetle (one move per minute) on the grid corresponds to many lines of FORTRAN in the simulation program. Consequently, when individuals are released for long periods of time, programs take several hours to run and to write results to other files. A limit was therefore placed on the number of individuals which could be released and on the duration of simulations.

The final data files were analysed using SPSS version 8.3 on the VAX mainframe computer to obtain the relevant parameters (the program is also capable of producing other data, not discussed here, such as the time of each encounter). The avoidance rate was checked for each species and the

proportion of individuals of each species encountering traps determined. As might be expected, a highly significant interspecific correlation was obtained between the actual avoidance rates and the avoidance rate recorded during each simulation. This implies that the FORTRAN random number generator is sufficiently accurate.

1008 beetles were released for each species at each different duration on the grid. This number was chosen because it was a common multiple of the number of individuals of each species for which data sets existed (9, 6 and 4) which was close to 1000. The results of these simulations, in terms of the proportion of the population encountering traps ($\bar{P}_{enc}$) for each different duration, are presented in Table 6.1. To save limited CPU time, movement of individuals of *Agonum muelleri* was not simulated at every duration because data for this species could not be used in later calculations.

It is clear from this table that the estimated proportion of individuals encountering traps ($\bar{P}_{enc}$) increases with time spent on the grid for each of the 5 species studied. Despite this trend, some of the individual results are difficult to explain e.g. the proportion of individuals of *B. quadrimaculatum* encountering traps over a period of 4 days is less than the figures for both 2 and 3 days.

Individuals of *P. melanarius* encounter traps at the highest frequency at all durations relative to other species and after 16 days the number of individuals of this species encountering traps is almost equivalent to the number of individuals on the grid. Indeed, the 'proportion' of individuals encountering traps exceeded 1 in a trial duration of 21 days for this species. This is possible because the population density is kept constant throughout simulations by replacing beetles trapped before the full duration has elapsed and because beetles which avoid traps can encounter traps again. $\bar{P}_{enc}$ is therefore not a true proportion and is most correctly referred to as the ratio of encounters to the number of individuals in the

Table 6.1

Results of simulations

Duration on grid (multiples of 12 hrs)	Ratio of the number of encounters to the number of individuals				
	<i>N. biguttatus</i>	<i>P. melanarius</i>	<i>B. quadrimaculatus</i>	<i>B. lampros</i>	<i>A. muelleri</i>
2	0,004	0,052	0,032	0,016	0,032
3	0,016	0,155	0,071	0,028	-
4	0,036	0,159	0,028	0,063	-
5	0,063	0,266	0,067	0,099	-
7	0,103	0,337	0,123	0,179	0,179
9	0,139	0,448	0,151	0,206	-
10	0,147	0,631	0,214	0,214	0,312
12	0,178	0,702	0,238	0,329	0,429
14	0,195	0,794	0,306	0,357	0,464
16	0,226	0,948	0,333	0,377	-

Table 6.2

Regression analysis of simulation data

Species	Independent variable	Dependent variable	Linear equation	r	d.f.	p
<i>N. biguttatus</i>	duration on grid (days)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$	$y=1,69x + 4,04$	0,9607	8	***
<i>P. melanarius</i>	duration on grid (days)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$	$y=4,17x + 7,56$	0,9914	8	***
<i>B. quadrimac.</i>	duration on grid (days)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$	$y=1,88x + 6,49$	0,9742	8	***
<i>B. lampros</i>	duration on grid (days)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$	$y=2,25x + 5,42$	0,9891	8	***
<i>A. muelleri</i>	duration on grid (days)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$	$y=2,83x + 5,14$	0,9949	3	***
All	Body length (mm)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$ (2x12hr.)	$y=0,52x + 5,43$	0,6498	3	NS
All	Body length (mm)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$ (7x12hr.)	$y=1,65x + 12,58$	0,9323	3	*
All	Body length (mm)	$\text{Sin}^{-1}\sqrt{\beta_{\text{enc}}}$ (14x12hr.)	$y=3,11x + 20,68$	0,9416	3	**

The mean value for body length was used for each species (see Table 4.3)

*** = $p < 0,001$ ** = $0,02 < p < 0,01$ * = $0,01 < p < 0,05$ NS = not significant ($p > 0,05$)

population.

The linear regression of $\hat{P}_{enc}$ (arcsine transformed) upon time spent on the grid is significant for each of the 5 species studied (Table 6.2).

There is also an interspecific positive linear relationship between the estimated proportion of individuals encountering a trap and the mean body length for each species (data from Table 4.3). This relationship was analysed statistically and shown to become more significant as the duration of time spent on the grid increases (Table 6.2).

There were four separate periods for which both pitfall trap data from the main sampling grid and quadrat (q) or mark-release-recapture (mrr) data were available from the field:

Period	Traps operated	Duration (days)	Number of traps	Population density estimates
1 'June 86'	3/6/86 - 17/6/86	14	30	11 - 12/6/86 (q)
2 'August 86'	5/8/86 - 4/9/87	28	30	12 & 22/8/86 (q) 11 - 15/8/86 (mrr)
3 'May 87'	29/4/87 - 27/5/87	28	20	6 - 27/5/87 (q)
4 'June 87'	27/5/87 - 17/6/87	21	20	3 - 12/6/87 (q)

All four periods occurred within the total pitfall sampling period for the year (see Chapter 2). "Digging-in" effects (Greenslade, 1964; 1973; Joosse & Kapteijn, 1968), where disturbance of the ground during the placement of new pitfall traps can act as an activity-stimulating phenomenon for several days afterwards, were therefore avoided.

A value of $\hat{P}_{enc}$ was required for each species for each of the four periods listed above. This is because both $\hat{P}_{enc}$ (from simulations) and N_{cap} (from the field) are related variables and are both dependent upon time. For example, in period 2, the pitfall traps in the field were operated for

a continuous period of 28 days. The value of $\hat{P}_{enc}$ is obtained for *Notiophilus biguttatus* by substituting 28 for x in the linear equation for this species (given in Table 6.2). It is necessary to square the sine of the y value obtained since the independent variable was arcsine transformed prior to regression. For *P. melanarius* in period 2 this involves splitting the y value before taking the sine since the value of y obtained when 28 is substituted into the equation is 124.32 which is greater than 90. In this instance, $[\sin(124.32 - 90)]^2 + [\sin(90)]^2$ was used to determine $\hat{P}_{enc}$.

Estimating $\hat{P}_{enc}$ from linear equations was deemed a more accurate method than simply using the value of $\hat{P}_{enc}$ obtained for 14 days by simulation (Table 6.1) since such values were liable to considerable variation. Using values for $\hat{P}_{enc}$ from the linear equations also involves extrapolation though, since both 21 and 28 days' duration are longer than the longest duration of simulation.

The value for $\hat{P}_{enc}$ obtained is then substituted into equation 3 (p. 197), along with the rate of avoidance from Chapter 4 (Table 4.3) and pitfall data from the field, to determine $\hat{N}_{cap}$, the estimated corrected number of individuals trapped. This is done for each species (except *A. muelleri*) in each period but shown in detail only for August 1986 data (Table 6.3).

In June 1986 the correlation between P_{cap} and P_A (the relative abundance expressed as a proportion) using arcsine transformed data is not significant (Table 6.5). However, when pitfall-trap data for this period are modified according to equation 3, the correlation between $\hat{P}_{cap}$ and P_A is significant ($0.01 < p < 0.05$) even though the number of degrees of freedom is only 1. The relative abundance of *N. biguttatus* in pitfalls is increased from 0.03 to 0.081 because of its high avoidance (relative to the other two species) and its relatively low probability of encountering traps. In other words, the species is underrepresented in pitfall traps in the field and the equation compensates for this by 'capturing' beetles in proportion to

their abundance. Similarly, *B. lampros* is underrepresented and *B. quadrimaculatum* overrepresented in pitfalls. The data for *B. lampros*, however, is adversely affected by the model since its modified relative abundance value ($\hat{P}_{cap}$) is not as close to P_A as was its unmodified (P_{cap}) value. The modification of data for *N. biguttatus*, and to a lesser extent *B. quadrimaculatum*, more than compensates for this adverse effect since the correlation coefficient is increased.

In August 1986, data on the absolute abundance of *P. melanarius* was available from mark-release-recapture studies. Since this species represents low avoidance and high activity rate (relative to the other three species studied) the correlation coefficient for the regression of P_{cap} upon P_A is very low (individuals of *P. melanarius* are overrepresented in pitfall traps in the field relative to the other species). Although modification of the data does not give a significant correlation between $\hat{P}_{cap}$ and P_A (Table 6.4), the correlation coefficient is increased from 0.2980 to 0.8696 at 2 degrees of freedom. As might be expected, it is the the pitfall data from the two 'extreme' species (*N. biguttatus* and *P. melanarius*) which are most greatly modified. This is because these species have the lowest (0.0811) and highest (1.1062) denominators in equation 3 i.e. $\hat{P}_{enc} \times [1-A]$.

The results for the other two periods are less encouraging (Table 6.5). In each case the modified pitfall-trap data give lower correlation coefficients when compared with relative abundance estimates than do the unmodified data, although in May 1987 the difference between the correlation coefficients is negligible. It should be noted that in these two cases the range of avoidance rates and probabilities of encountering traps is narrower than for August 1986 when *P. melanarius* was included in the data set and in neither case does the modification take the correlation coefficient from a level of statistical significance to one of no statistical significance. This explanation, however, is not consistent with

the significant correlation found for June 1986 data.

Correlation between P_{cap} and P^A and between $\hat{P}_{cap}$ and P^A over the whole data set (combining data from all four periods) gives values of 0.7189 (r_1) and 0.7943 (r_2) respectively. Both, at 11 degrees of freedom, are statistically significant but there is a stronger correlation between modified population estimates and actual abundance estimates than there is between pitfall trap data and actual abundance estimates ($0.001 < p < 0.01$ (r_1) and $p < 0.001$ (r_2)).

Even though the correlation coefficients are not significant for three of the periods, the predictions of absolute abundance, being the ultimate aim of the study, are given (Table 6.6). It is clear that the higher the correlation coefficients in Tables 6.4 and 6.5, the closer are these estimates to the actual abundance estimates from quadrat and mark-release recapture studies. In most cases, the difference between the two estimates is less than one beetle per square meter although this can represent a relatively high percentage error because of the low population densities. The implications of this degree of inaccuracy in terms of the usefulness of the technique in future integrated pest management situations will be discussed further in Chapter 7. The degree to which the predictive approach can be improved, and the two estimates presented in Table 6.6 brought more closely together, will be discussed in Section 6.4.

Table 6.3

Estimation of $\hat{N}_{cap}$ for four species of Carabidae, August 1986.

Species	P_{enc}	[1-A]	N_{cap}	$\hat{N}_{cap}$
<i>N. biguttatus</i>	0.6101	0.1333	7	86.07
<i>P. melanarius</i>	1.3179	0.8394	341	308.23
<i>B. quadrimaculatum</i>	0.7367	0.3694	83	304.99
<i>B. lampros</i>	0.8647	0.1977	46	269.08

P_{enc} = proportion of individuals encountering traps in 28 days, Estimated from regression equation in Table 6.2

A = proportion of individuals avoiding traps (Table 4.3)

N_{cap} = Number of individuals captured in pitfall traps in the field during August 1986

$\hat{N}_{cap}$ = estimated number of individuals captured in pitfall traps (equation 3)

$$\hat{N}_{cap} = N_{cap} / (P_{enc} * [1-A]) \quad (3)$$

Table 6.4

Correlation of pitfall data and modified pitfall data with relative abundance
August, 1986.

Species	No. /m ²	P _Δ	N _{cap}	P _{cap}	N _{cap}	P _{cap}
<i>N. biguttatus</i>	1.26	0.089	7	0.015	86.07	0.089
<i>P. melanarius</i>	3.26	0.232	341	0.715	308.23	0.318
<i>B. quadrimaculatum</i>	5.75	0.409	83	0.174	304.99	0.315
<i>B. lampros</i>	3.80	0.270	46	0.096	269.08	0.278

r1 = 0.2980; d. f. =2; p>0.05

r2 = 0.8696; d. f. =2; p>0.05

No. /m² = absolute abundance data from quadrats or mark-release-recapture.

P_Δ = proportional abundance of species listed.

N_{cap} = number of individuals captured in pitfall traps in the field in August 1986

P_{cap} = proportional abundance (of species listed) in pitfall traps in the field in August 1986

N_{cap} = estimated number of individuals captured in pitfall traps.

P_{cap} = estimated proportional abundance (of species listed) in pitfall traps

r1 = correlation coefficient for correlation between $\sin^{-1} \sqrt{P_{cap}}$ and $\sin^{-1} \sqrt{P_{\Delta}}$

r2 = correlation coefficient for correlation between $\sin^{-1} \sqrt{\hat{P}_{cap}}$ and $\sin^{-1} \sqrt{P_{\Delta}}$

Table 6.5

Correlation of pitfall data and modified pitfall data with relative abundance

June 1986 (period 1)						
Species	No. /m ²	PA	N _{cap}	P _{cap}	N _{cap}	P _{cap}
<i>N. biguttatus</i>	0.50	0.223	7	0.03	243.00	0.081
<i>B. quadrimaculatum</i>	0.62	0.277	72	0.31	663.86	0.221
<i>B. lampros</i>	1.12	0.500	150	0.65	2102.90	0.699

r1 = 0.9315; d. f. =1; p>0.05

r2 = 0.9969; d. f. =1; 0.01<p<0.05

May 1987 (period 3)						
Species	No. /m ²	PA	N _{cap}	P _{cap}	N _{cap}	P _{cap}
<i>N. biguttatus</i>	0.08	0.037	9	0.023	110.66	0.058
<i>B. quadrimaculatum</i>	0.92	0.422	189	0.487	694.50	0.362
<i>B. lampros</i>	1.18	0.541	190	0.490	1111.43	0.580

r1 = 0.9849; d. f. =1; p>0.05

r2 = 0.9842; d. f. =1; p>0.05

June 1987 (period 4)						
Species	No. /m ²	PA	N _{cap}	P _{cap}	N _{cap}	P _{cap}
<i>N. biguttatus</i>	0.13	0.059	9	0.021	166.71	0.054
<i>B. quadrimaculatum</i>	1.27	0.577	167	0.386	874.44	0.282
<i>B. lampros</i>	0.80	0.364	257	0.593	2056.88	0.664

r1 = 0.8082; d. f. =1; p>0.05

r2 = 0.5996; d. f. =1; p>0.05

No. /m² = absolute abundance data from quadrats.

PA = proportional abundance (of species listed) in quadrats.

N_{cap} = number of individuals captured in pitfall traps in the field.P_{cap} = proportional abundance (of species listed) in pitfall traps in the field.N_{cap} = estimated number of individuals captured in pitfall traps.P_{cap} = estimated proportional abundance (of species listed) in pitfall trapsr1 = correlation coefficient for correlation between $\sin^{-1} \sqrt{P_{cap}}$ and $\sin^{-1} \sqrt{PA}$ r2 = correlation coefficient for correlation between $\sin^{-1} \sqrt{\hat{P}_{cap}}$ and $\sin^{-1} \sqrt{PA}$

Table 6.6

Predictions of absolute abundance from $\hat{P}_{cap}$

Species	Date	$\hat{P}_{cap}$	$\hat{\Delta}$ no. individuals per m ²	$\hat{\tilde{\Delta}}$ no. individuals per m ²
<i>N. biguttatus</i>	June 86	0.081	0.50	0.18
<i>B. quadrimaculatum</i>	June 86	0.221	0.62	0.50
<i>B. lampros</i>	June 86	0.699	1.12	1.57
$\sum_{i=1}^s \hat{\Delta}_i$			2.24	
<i>N. biguttatus</i>	Aug 86	0.089	1.26	1.27
<i>P. melanarius</i>	Aug 86	0.318	3.27	4.47
<i>B. quadrimaculatum</i>	Aug 86	0.315	5.75	4.43
<i>B. lampros</i>	Aug 86	0.278	3.80	3.91
$\sum_{i=1}^s \hat{\Delta}_i$			14.07	
<i>N. biguttatus</i>	May 87	0.058	0.08	0.13
<i>B. quadrimaculatum</i>	May 87	0.362	0.92	0.79
<i>B. lampros</i>	May 87	0.580	1.18	1.26
$\sum_{i=1}^s \hat{\Delta}_i$			2.18	
<i>N. biguttatus</i>	June 87	0.054	0.13	0.12
<i>B. quadrimaculatum</i>	June 87	0.282	1.27	0.62
<i>B. lampros</i>	June 87	0.664	0.80	1.46
$\sum_{i=1}^s \hat{\Delta}_i$			2.20	

$$\hat{\tilde{\Delta}} = \hat{P}_{cap} * \sum_{i=1}^s \hat{\Delta}_i \quad (5)$$

$\hat{P}_{cap}$ = estimated proportional abundance (of species in group) in pitfall traps

$\hat{\Delta}$ = estimated population density from quadrats or mark-release recapture

$\hat{\tilde{\Delta}}$ = estimated population density from equation (5)

s = the number of species in the group for each date

6.4 Discussion

6.4.1 Discussion of results

Simulation of activity data gives the parameter $\hat{P}_{enc}$ for each species released on the grid. This is the estimated proportion of individuals encountering traps in the field or the probability of any one individual in the population encountering a trap.

The value of $\hat{P}_{enc}$ increases with the time spent on the grid, as might be expected from the Brownian theory of motion. Regression of $\hat{P}_{enc}$ (dependent) on duration (independent) gives a significant linear relationship for each species (Table 6.2). Some individual results in Table 6.1 are difficult to explain e.g. the small difference between $\hat{P}_{enc}$ for durations of three and four days for *P. melanarius* and the low value for $\hat{P}_{enc}$ for 4 days for *B. quadrimaculatum*. Unfortunately, time was not available to rerun the simulations and these data were used in the final modification of pitfall data since estimates of $\hat{P}_{enc}$ were obtained from linear equations derived from them. These aberrations would perhaps benefit from running the simulations once more using a different random number sequence.

The maximum duration of simulations was sixteen days and no simulations were run for several of the intermediate days. Values for $\hat{P}_{enc}$ can be obtained for intermediate or longer durations by simple adjustment to the program presented in Appendix 4 (a copy of the data file is available). Ultimately, estimation of $\hat{P}_{enc}$ should simply be a matter of substituting the required duration in the linear equation for the species but data from intermediate durations would improve the accuracy of this equation.

There is an interspecific relationship between body length and $\hat{P}_{enc}$

which increases in significance with increasing duration on the grid. It could therefore be tentatively concluded that the probability of an individual encountering any trap in an identical grid and for a specific duration can be predicted from the mean body length of the species alone. If this were the case then the simulation would become unnecessary. However, I consider that more data on activity patterns need to be collected and further simulations carried out before any firm conclusions can be reached. The relationship presumably breaks down at shorter durations of simulation (i. e. less than 2 days) because very few or no individuals of the slower-moving species encounter traps. This should not be a problem in terms of eventually using the technique to predict absolute population density from pitfall trap data since most workers operate pitfall traps for periods greater than a few days and the duration of simulation should ideally be equivalent to this period.

The modification of pitfall trap data in Table 6.3 and for any of the other periods is dependent upon the duration for which traps were operated in the field. The equivalent duration is substituted into the linear equation for each species presented in Table 6.2 and the value of $\hat{P}_{enc}$ obtained is used in equation 3 (presented below Table 6.3). It is clear from this table that the proportion of the population captured ($\hat{P}_{enc} * [1 - A]$) is greater than one in period 2 (August 1986) for *P. melanarius*. The source of this anomaly is the high value of $\hat{P}_{enc}$ which is possible because a constant population density is continually sampled (some beetles encounter traps more than once). This results in a value for $\hat{N}_{cap}$ which is lower than the actual number of beetles captured in the field! This might at first sight seem unrealistic but the estimate of $\hat{P}_{enc}$ was arrived at by simulating beetle movement for a continuous period of 12 hours each day. If this is an overestimate (likely since *P. melanarius* is nocturnal and there are less than 12 hours of darkness each day in August) then $\hat{P}_{enc}$ will be an

overestimate. For the three diurnal species, $\hat{N}_{cap}$ exceeds N_{cap} since none of the values of $\hat{P}_{enc}$ exceed unity. This does not necessarily mean that the values for $\hat{P}_{enc}$ for these species are accurate; the basic assumption that the 15-minute activity patterns of individuals of these species are continually repeated for 12 hours each day might also lead to an overestimate.

The most striking figures in Table 6.3 and 6.4 are those of $\hat{N}_{cap}$, which can best be described as the number of individuals which would have been captured if all individuals in the population encountered traps and each species had a 0% avoidance rate. In some cases the numbers are extremely high but $\hat{P}_{cap}$ is a hypothetical parameter which is simply an intermediate stage necessary to ultimately determine population density. Nevertheless, if $\hat{N}_{cap}$ values are divided into the area of the sampling grid in the field, then realistic population densities are obtained. These range from 0.11 to 0.41 individuals/m² for the four species studied in August 1986 if it is assumed that the sampling area of 30 traps is 750m². These values, although typical of carabid abundance estimates (Thiele, 1977) are much lower than the actual abundance estimates recorded for this period from quadrat and mark-release-recapture data (1.26 to 5.75 individuals/m²), a difference which is difficult to explain.

The area of influence of a grid of pitfall traps in the field is difficult to quantify and the value given above was arrived at by making the boundary of the grid 2.5m from the outer traps (this is half the distance between traps and between rows of traps). If this was an overestimate then the values for population density given above will be underestimates. This explanation alone does not account for the magnitude of the difference though. The relocation of beetles which avoid traps in simulations was achieved by adding 0.353m to both x and y coordinates i.e. they were relocated 0.5m from the trap. This was to prevent beetles

encountering the same trap on completion of the next move since such behaviour was rarely observed in experiments described in Chapter 4. Because of this prerequisite, this distance was to a certain extent artificial (beetles do not suddenly move 0.5m from a trap following an avoidance response but their actual behaviour is too complex to simulate) and may have made the rate at which individuals encountered traps artificially high. This in turn would result in a lower estimate of $\hat{N}_{cap}$. Other explanations are possible: the population density estimates from the field are not based on continuous sampling throughout the period and may be overestimates; activity of beetles was simulated for 50% of the 24 hour period and if this is an overestimate (see above) then the values of $\hat{P}_{enc}$ from simulations will be overestimates too, resulting in underestimated values for $\hat{N}_{cap}$.

Nevertheless, correlation between the untransformed variables gives only a slightly lower correlation coefficient than when arcsine transformed relative abundance estimates are correlated. This implies, at least for August 1986, that all values of $\hat{N}_{cap}$ have been underestimated to a similar degree.

These criticisms of the magnitude of the parameter $\hat{N}_{cap}$ are to a certain extent superfluous since the important parameter is $\hat{P}_{cap}$, because it is used to predict absolute population density. Using $\hat{P}_{cap}$ is more reliable because it is a relative estimate of abundance and can be directly compared with P_A . It also removes the necessity to incorporate the area of influence of a grid of pitfall traps in the field which is difficult to determine: the hypothetical parameter $\hat{N}_{cap}$ is simply a means to an end.

In the introduction to this chapter, an alternative approach to the problem of assessing the effectiveness of the theory behind equation 3 was considered. It was suggested that beetle movement could be simulated by releasing individuals according to the relative abundances of species. The

number of individuals captured in simulations could then be compared directly with the number of individuals captured in the field during the same period over which the absolute abundance estimates were made. The approach was rejected in favour of the predictive approach because of the latter's likelihood of being used in the future. However, there are other problems associated with the use of the former approach:

1. If a group of species is being studied and one species has a very low population density relative to another, the activity of a very large numbers of individuals of the latter would have to be simulated in order to simulate the activity of enough individuals of the least abundant species for statistical analysis. The running time of simulations involving many individuals is a prohibitive factor in this respect and likely to be so on most mainframe computer systems for some years to come.
2. Using the approach adopted in the present study, once the probability of an individual of a particular species encountering a trap ($\hat{P}_{enc}$) has been accurately determined by simulation, no more simulations need to be run. This is because the parameter $\hat{P}_{enc}$ is independent of population density. Using the alternative approach, simulation of movement at many different population densities would be necessary for every comparison between the number of beetles captured in simulations and the number of individuals captured in the field.

The predictive approach was chosen since it is a technique which can be tested for accuracy *and*, with further refinements, be used to estimate absolute abundance from pitfall-trap data.

Tables 6.4, 6.5 and 6.6 conclude the summary aims outlined in Chapter 1 (p.16). The estimated relative abundances of species in pitfall traps

(β_{cap}) presented in Tables 6.4 and 6.5 are used to predict absolute abundances of species in Table 6.6. The accuracy of the parameter β_{cap} was determined by correlation with absolute population density estimates. The degree of accuracy is not as good as was expected, some of the reasons for which have been discussed above e.g. insufficient interspecific differentiation in body length and some of which are inherent in the simulation itself and will be discussed below in Section 6.4.2. Consequently, the predictions of absolute abundance are also inaccurate. These results, and an overall evaluation of the predictive approach both with respect to this study and for its use in the future, will be discussed in Chapter 7.

6.4.2 Simulation of movement

The simulation is simplistic in many respects but is still of use. It was developed to maximise versatility in use (e.g. with respect to setting parameters and the input and output of data). Its accuracy could certainly be improved with further thought and expanded use.

Kitching (1971) advocates the practice of gradual development of simulation models by incorporating initial assumptions. Siniff & Jessen (1969) describe a similar method of construction of a simulation model of movements of mammals using parameters derived from telemetric field data. Such an approach was adopted throughout the development of the present simulation (1984-1987) but it is conceded that further improvement is necessary.

Although similar, the present simulation model is more realistic than that of Kitching (1971) in that it uses actual field data on activity: Kitching used a normal distribution to determine deviation per unit time and a constant spatial displacement per unit time.

In the present study, the use of the mean values for velocity and deviation was considered. It was thought that there would not be a

straightforward relationship between mean velocity and the chance of encountering a trap, this is because the traps were regularly distributed and so would be the coordinates of consecutive positions of individual beetles.

It is necessary to discuss the various major assumptions which are incorporated into the simulation model:

1) Mortality

It is assumed that population density remains constant for the duration of release on the grid. Such an assumption can be justified to a certain extent. The quadrat samples were taken on various occasions during each relevant period and although no mean values are given for population density in Chapter 3, the estimates should be representative of the population density throughout the period. The estimate of the population density of *P. melanarius* was probably less accurate since it was made between 11th and 15th August whereas the pitfall data for Period 2 ('August 86'), which is dependent upon population density in the vicinity of the traps, was collected between 5th August and 4th September.

The assumption that population density remains constant in the field is clearly unrealistic but its consequences, in terms of the final prediction of population density, can be minimised by decreasing the duration of simulations and the duration over which pitfall trap data is collected. This is because population density fluctuations increase with time. A compromise needs to be reached though between reducing innacuracy inherent in the assumption that population density remains constant temporally and increasing the number of individuals captured in the field (N_{cap} increases with the number of days traps are operated). The latter could be reduced if the number of traps used is increased (but less than 10 individuals of *N. biguttatus* were taken by 30 traps over a period of 28 days

(cf. Table 6.5) so many more traps would be required to satisfy the assumption of constant population density whilst keeping N_{cap} sufficiently high. Also, more traps would cover a greater area and make any assumption of uniformity of distribution less justifiable.

The alternative approach would be to incorporate population density fluctuations in the simulation but this would be counterproductive for two reasons:

i. Each estimate of $\hat{P}_{enc}$ for a species is independent of population size since it is the probability of an individual beetle encountering a pitfall trap and, consequently, the proportion of the population which encounters traps. $\hat{P}_{enc}$ would therefore be unaffected by fluctuations in the number of other individuals released. The number of individuals released does need to be a constant high value in order to accurately determine $\hat{P}_{enc}$

($=N_{enc}/N_{rel}$).

ii. The aim of the simulation is to predict population densities, not to laboriously determine them over a period of time before simulations are performed.

2) Step-over

The coordinates of an individual beetle were only checked by the FORTRAN subroutine at the end of every move (i.e. after each simulated minute of activity). It is possible that a beetle could pass over the critical coordinates (those corresponding to the trap) during one of these moves and be located at uncritical coordinates at the completion of the move.

It has been pointed out that simulations of in excess of one thousand individuals moving about the grid for several days take many hours to run. To check of the coordinates of each beetle between moves would considerably

increase the running time of the program. At Leicester, a limit was placed on the amount of C.P.U. allowed by each mainframe user. The assumption cannot be criticised too fully because such criticism is based on yet another assumption - that beetles in the field travel in a straight line between two consecutively recorded positions. The limitation therefore lies in the method of collection of field data rather than in the construction of the simulation model. Even so, by decreasing the time between observations in the field simulations would take much longer to run e.g. if the time between observations was reduced to 10 seconds, simulations would take approximately 6 times as long to run.

The consequence of such an assumption as it stands is that $\hat{P}_{enc}$ is likely to have been underestimated due to the occasions when non-detection of a beetle's coordinates being critical ones occurred. Nevertheless, because the parameter is a relative one interspecifically, and is not used in any absolute sense, such an underestimate is not as crucial as it might seem. Also, the number of occurrences of such situations is likely to be similar when it is compared interspecifically although there will be a trend upwards with increasing body length. This is because larger species move greater distances than smaller species and are likely to have a greater probability of 'missing' a trap in simulations as a consequence.

3) Duration

Each data set represents only fifteen minutes of activity in the field for an individual beetle. The number of data sets per species was also low (between four and nine). It is assumed that a beetle's total activity for each day may be extrapolated from its activity over fifteen minutes. It was also assumed that the individuals for which data existed were representative of their respective species. Finally, it was assumed that each species repeated the observed activity patterns for 12 hours each day. This final assumption was necessary since no data was available on the

duration of activity of species i.e. the proportion of the 24-hour day spent active. This is likely to differ interspecifically with respect to factors such as prey handling time determining the magnitude of the proportion of the day individuals devote to locomotor activity (species which exhibit extraintestinal digestion of prey for example, are likely to have relatively long handling times).

These assumptions involving the extrapolation of activity data are clearly the most unrealistic of the assumptions built into the simulation and should be improved in future by increasing both the duration and number of replicates of individual data sets and by incorporating independent data on the proportion of the 24 hour day during which individuals are active. In experiments to determine diel periodicity of species (Chapter 3), the traps were only emptied at dawn and dusk and so this was not possible. More accurate estimates of diel activity patterns could be obtained by using time-sorting pitfall traps.

Nevertheless, only by attempting such a simulation does one come to realise its limitations and potential for improvement.

4) Relocation

Beetles were relocated on the grid if they encountered and then avoided a pitfall trap. Many hours of direct and indirect (using a video camera) visual observations of beetles encountering pitfall traps allow me to conclude (although this conclusion is not based on any quantitative assessment) that beetles avoiding a trap rarely re-encounter the same trap immediately afterwards. It is therefore difficult to reposition beetles immediately after such an encounter during simulation. (The program would register continuous encounters unless the pattern of movement being read in from the data file positioned the beetle elsewhere). The value chosen was a compromise between the necessity to prevent multiple encounters and to minimise the reduction in the final rate of encounter which might result

from constantly positioning individuals too far away from traps subsequent to an avoidance response.

The program also allows relocation if individuals were trapped or reached the edge of the grid but the latter situation will only occur for particularly long durations (it can also be avoided by increasing the size of the grid - a simple modification to the program).

Chapter 7

General Discussion

Pitfall traps facilitate the simultaneous study of a number of habitats revealing species composition; they allow the analysis, intraspecifically, of annual rhythms of activity; they are useful in comparing diel periodicity patterns interspecifically; they can be used to determine patterns of distribution (contagious, regular, random) within a uniform habitat and considered alone, they are superior to all other methods of sampling populations of carabid beetles.

They are frequently misused however, particularly when intraspecific inter-habitat comparisons of abundance are made (e.g. Pollard, 1968; Drach & Faille, 1981; Los & Allen, 1983; Jennings *et al.* 1986 - see Chapter 1). They cannot be used in such a way because the environmental resistance to movement differs between habitats and consequently the rate of encounter with pitfall traps is not equivalent at equal population densities. Unless such differences can be taken into account, one must rely on absolute estimates of abundance e.g. the use of quadrats and soil extraction (Desender, 1982).

Within the same habitat, pitfall traps can be used to compare intraspecific relative abundances with respect to time. Their major disadvantage is the problem of obtaining valid interspecific relative abundance estimates from pitfall-trap captures alone. This is due to interspecific differences in activity patterns and, as the present study has revealed, interspecific differences in behaviour upon encountering a pitfall trap (pitfall-trap avoidance). Species are clearly not trapped in proportion to their abundance.

Other factors include the relative attractive qualities of the preservative fluid used in traps (e.g. Luff, 1968) and the type of trap used (e.g. Luff 1975; Waage, 1985). However, if a preservative fluid such as ethane diol is used, and traps of uniform design are utilised (the avoidance parameter takes into account the design of the trap), then only activity and avoidance remain as the two parameters which must be quantified before pitfall-trap data can be used to obtain relative population estimates within the Carabidae.

Because of interspecific differences in avoidance and locomotor activity rates, most researchers find that species of Carabidae are not captured in proportion to their abundance (Skuhravy, 1957b; Briggs, 1961; Lesiewicz *et al.* 1983 and others). The few papers which report close agreement between absolute abundance estimates and pitfall trap captures seem to have considered species of similar body length. Schütte (1957) studied 10 species of Carabidae in a forest in northern Germany. A DDT campaign aimed at destroying *Tortrix viridana* L. was so effective that it killed the entire carabid population too. The percentage distribution of dead individuals of each species was compared with the results from baited traps which had been in position in the same area for some time and close agreement was found. The ten species included *Calosoma* (1) *Carabus* (3) *Pterostichus* (3) *Abax* (2) and *Agonum* (1). These genera all contain species of similar body lengths and presumably, as the present study suggests, similar avoidance rates and locomotor activity patterns. A similar fortuitous association seems to have been arrived at by Dubrovskaya (1970) in her study of the Carabidae of arable land in the USSR.

Several attempts have been made to overcome the problem of linking pitfall trap captures to relative density in the field, although so far these have only considered differences in activity. The concept of activity density (Heydemann, 1953) or activity abundance (Tretzel, 1955) was one of

these discussed in Chapter 1. In that chapter I criticised its value in describing the ecological role of a predatory species in a community, because it did not take into account other factors involved in a predator's search for its prey: the most efficient predators are not simply the most active. Adis (1979) in a comprehensive review of pitfall methodology also criticised the use of activity-dominance indices.

It is now clear that species avoid pitfall traps at different rates, and that there is a greater difference between species than was originally suggested by Luff (1975). Two species such as *Pterostichus melanarius* and *Bembidion lampros* illustrate the problem of using activity dominance indices. Both species feed on aphids at a similar rate (Sunderland & Vickerman, 1980; Chiverton, 1987) and occur in cereal crops together. To incorporate the activity abundance index into an integrated pest management program in future years could give the wrong impression as to the relative effectiveness of the two species. Individuals of *P. melanarius* have a relatively high rate of locomotor activity and a low rate of pitfall trap avoidance relative to *B. lampros*. This difference in activity rate is taken into account by the index but the difference in avoidance rates (16.06% and 80.23% respectively) would give an even higher index to the former species. A recent paper (Hokkanen & Holopainen, 1986) used the index on these two species and drew conclusions about their relative abundance in cabbage fields. Consequently, *P. melanarius* was referred to as the dominant species, a conclusion based upon the number of individuals captured in pitfall traps alone.

Many studies still equate pitfall-trap captures to activity abundance (e.g. Fox, 1974; Dritschilo & Wanner, 1980; Boiteau, 1983; Susdiko & Pisarenko, 1983; Varis *et al.* 1984; Ferguson & McPherson, 1985; Knauer & Stachow, 1987 and many others) thereby failing to recognise the interspecific differences in avoidance rate.

It could be argued that this problem could be overcome by simply

taking into account the different rates of avoidance to give a more realistic activity abundance index. However, the other criticism of the index, that it is unrealistic when regarded as a description of the role of a predatory species must not be overlooked. For example, two of the species studied here have specialized predatory techniques which do not rely on constant locomotor activity. *Loricera pilicornis* uses its antennae as setal trap to capture prey (Hintzpeter & Bauer, 1986) for which it lies in wait. *Notiophilus biguttatus* relies heavily on visual acuity for capturing prey (Bauer *et al.*, 1977) which it actively locates. These strategies are thought to have evolved in response to the escape behaviour of Collembola (springtails), of which both species are predators. Nevertheless, both species are also aphidophagous to some extent but it is likely that they adopt a similar pattern of locomotion for this type of prey despite the ease with which aphids can be captured. Empirical support for this statement comes, at least for *N. biguttatus*, from many hours of observation of individuals in the field - its characteristic movement pattern of short dashes followed by longer pauses is always maintained.

Den Boer (1971; 1977) and Meijer (1974) show that pitfall-trap captures can be used to give intraspecific relative population estimates with respect to time. Seasonal activity patterns of most species have been demonstrated in this way by many workers with the peak abundance taken as the time at which the greatest number of individuals are taken in a standard set of pitfall traps. However, it is often necessary to compare relative abundances between species. Baars (1979a) has suggested that a positive linear relationship exists between the number of individuals of a species captured throughout a prolonged period and the mean density of the species throughout the same period and that by remodelling data from the literature and simulating beetle movement on a grid of pitfall traps, he revealed that continuous pitfall trapping throughout the year can

eventually give an indication of interspecific relative population densities.

Such an approach is not always possible, particularly in arable crops where short-term forecasting of population density might be required at the start of the spring (corresponding to the aphid's pre-peak period in many cereal crops). Only if data from previous years are available can the method proposed by Baars (1979a) be adopted. Even so, as Luff (1982b) has pointed out, this depends on the same crop being planted in the field from year to year since relative population densities within the Carabidae can be crop-dependent. What will be required in most agricultural pest situations is a more rapid method of estimating relative abundances.

Sunderland *et al.* (1987b) present a method of estimating densities which is based upon the utilisation of a range of sampling techniques in a specified area of crop. They argue that all methods of sampling are subject to various biases but that if a variety of methods are used then all animals can be removed from a fixed area. The four methods employed are vacuum insect net, plant search, ground search (using a quadrat) and the use of pitfall traps in enclosures (trapping out). The percentage of the total catch of carabids that was due to each sampling method used in isolation was calculated and it was shown that each method underestimated predator density but by combining sampling methods, a more accurate estimate of absolute density is achieved. The authors acknowledge that such an approach is very labour intensive (nine man-hours for each square meter of ground). Many species occur at densities of only a few individuals m^{-2} (see Chapter 3) and so many samples would have to be taken to achieve high enough numbers for statistical comparisons to be made.

The authors found that the single most efficient method was enclosed pitfall traps over a period of 7 days (up to 84.1% of predators captured). Such a method has been used by other workers over longer periods to completely 'trap out' an area (e.g. Gist & Crossley, 1973; Desender *et al.*

1982; Desender & Maelfait, 1986). This too can be time consuming and costly in terms of depleting an area of the beetles which are being studied. It was argued in Chapter 3 that quadrat sampling is too time consuming for obtaining estimates of absolute population densities of most species of Carabidae, and is particularly unsuitable for nocturnal species. It should ideally be combined with some form of extraction from the soil but this has the added disadvantage of disturbing both the crop and the soil surface and necessitates handling large amounts of soil.

Other advocates of the holistic approach include Kowlski (1975) "Obtaining valid population indices from pitfall trapping data". This paper is disappointing in that its contents do not support the promising statement of the title: intraspecific relative abundance estimates only are given. Novak (1971b) only partially tackles the problem of achieving population density estimates from pitfall trap data. A translation of his paper could not be obtained but an English summary suggests that the paper is mainly a discussion of the problem and concludes that by studying diel periodicity and beetle activity patterns more realistic abundance estimates could be arrived at.

The only other holistic approach to this problem has been by Jansen & Metz (1979). Their theoretical study separates out the three main parameters activity, avoidance and population density (although they do not use the term avoidance and do not define it as it has been defined in the present study). Although the mathematical steps presented in the paper are extremely complex and must be beyond most ecologists, it was a useful starting point for the present study. Introductory statements such as the following proved useful: "The number of parameters characterizing a particular model should be as small as possible, however. One should preferably, be able to estimate these parameters in separate experiments, so that the performance of the model may be evaluated." (p.99). Such an approach was adopted during the present study and it is thought that the

success of the predictive model depended on its simplicity.

The number of species for which data for all three parameters were collected (activity, avoidance and population density) was somewhat low. Time was the limiting factor: The original aim of the study was to investigate avoidance behaviour but as the study progressed, an holistic approach to the problem of predicting interspecific relative abundance from pitfall-trap data only became apparent at a much later stage. As a consequence, the final assessment of the success of the approach (Chapter 6) was limited. Application of the model to pitfall-trap data in Chapter 6 actually reduces the correlation coefficient on both sets of data for 1987. This should not cause too much concern when it is considered that in both cases the three species are of similar body length (implying that they show relatively little differentiation with respect to avoidance and locomotor activity rates). In retrospect it would have been better to study species representing a wider range of body lengths, but when the species were originally chosen, the relationships between body length and both avoidance and locomotor activity rates (and hence $\hat{P}_{enc}$ - the proportion of individuals encountering traps) were not foreseen.

Only in one instance was a data set available which included beetles of the two extremes of body length (Period 2; August 1986). Here, the correlation coefficient is low (0.2980 at 2 d.f.; $p > 0.05$) when the relative abundance of species in pitfall traps in the field (P_{cap}) is correlated with relative abundance in the field (P_A) (in correlation, it is the arcsine of each of these values that is used, but for convenience, the proportional values will be quoted). On the application of the model, i.e. equations 3 and 4, to the pitfall data, the relationship between the two variables $\hat{P}_{enc}$ (the estimated relative abundance of species in pitfalls) and P_A approaches significance since the correlation coefficient is increased (0.8696 at 2 d.f.; $0.05 < p < 0.1$).

The fact that the relationship is not significant is perhaps due to

the low number of species tested during the same period and the various assumptions associated with the simulation of movement. I am still confident that the model will be most useful under circumstances when species of different body length are being compared. In situations where beetles of similar body length are studied (the other three periods in Table 6.5) beetles are more likely to be captured by pitfall traps in the field in proportion to their abundance. This was demonstrated in Chapter 6 where a high correlation coefficient was found between actual abundance and unmodified pitfall-trap captures on two out of three occasions. Similar results, it is argued above, were achieved by Schütte (1957) and Dubrovskaya (1970).

It is perhaps because three out of the four data sets contain species of similar body length that when P_{cap} is regressed upon PA for all the data presented in Table 6.3, a significant correlation is found ($r=0.7189$ at 11 d.f., $0.001 < p < 0.01$). Nevertheless, application of the model to all data sets together (regression of $\hat{P}_{enc}$ upon PA) results in a slightly higher, and more significant correlation coefficient ($r=0.7943$, $p < 0.001$).

Interspecific relationships between $\hat{P}_{enc}$ and mean body length were also found and it is tempting to slot other species into the model without collecting the relevant field data on locomotor activity. This is not to be encouraged since very few species were investigated in this study and the relationship may be a fortuitous one. If the relationship does hold after further investigation i.e. if the probability of encountering pitfall traps in the field can be predicted from body length alone, then the model could be applied to pest management situations rapidly and without the collection of field data specific to the situation.

The results presented in Chapter 6 suggest that the approach adopted in the present study is likely to be a successful one when applied to data sets containing species of differing body size. Nevertheless, the fact that the correlation coefficient (Table 6.4) is not significant suggests there

is room for many refinements. The most important of these will now be considered in turn.

The accuracy of the results from the simulation model will be dependent upon the quality of the activity data collected from the field. If only a few individuals of each species are studied then the data are unlikely to be representative of the population as a whole. The duration for which each individual is followed in the field will determine how representative the data set for that beetle is for its activity throughout the day (or night). The 15-minute observation period chosen in the present study is possibly somewhat short. However, as the observation period is extended, problems are encountered e.g. the chance of an individual beetle being lost increases. The time interval between successive observations of the beetle's position (60 seconds in this study) determines the accuracy of parameters such as mean velocity, actual distance and mean deviation, but if this interval is shortened, the possibility of disturbing the beetle, and thus affecting the results, increases. I consider that 60 seconds is a suitable compromise.

Extrapolation of activity data is essential if beetle movement is to be simulated for long periods. Individual data sets are short out of necessity since it is too time consuming to pursue individual beetles in the field for hours on end. Inaccuracy is also inevitable unless data are available on the duration of diurnal activity periods i.e. for what proportion of each 24-hour period beetles of each species are active. This was not attempted in the present study, instead, the assumption that all species are active for 12 hours each day was incorporated into the simulation. To accurately quantify such a parameter is likely to be a complex task since it is dependent upon a number of factors e.g. the climate and the physiological state of the insect. The problem of the effect of climate could be simplified if it could be shown that changes in

ambient temperature affect all species equally. A somewhat simpler refinement would be to incorporate the relative lengths of the light and dark phases of the day for a particular time of year into the simulation. This could be done by controlling the relative duration of the activity of nocturnal and diurnal species during simulations.

As argued earlier with respect to locomotor activity, the model will be most successful when species of similar body form (Forsythe, 1987b) are studied. The majority of carabid beetles which are known to feed on aphids, and for which the model will be most applicable, are of similar body form. Exceptions, such as *Loricera pilicornis*, which is considered a faster runner than would be expected from its body form alone (Forsythe, 1987b), are unlikely to disrupt the model greatly. Species of distinctly different body form, e.g. *Clivina fossor* L., and consequently different habit (Desender, 1983) should be excluded from such a model.

The relationship between body length and locomotor activity (Chapter 5) is based on data for only five species and merits further study. However, it is of little use in the model since it only predicts mean velocity from body length. As explained in Chapter 6, mean velocity is of little use in simulations since it involves the imposition of a regular parameter upon a regular grid of pitfall traps. Successful simulation depends on the actual inputting of field data move by move and so the results, in terms of the proportion of individuals encountering traps, cannot be predicted from body length alone. (Simulation of movement also relies on data relating to the angular deviation as well as velocity and this could not be predicted from body length in Chapter 5).

However, the results of simulations suggested that body length might be related to the probability of encountering a pitfall trap ($\hat{p}_{enc}$). If this still proves to be the case when more data has been simulated, then the prediction of $\hat{p}_{enc}$ from body length would replace the need to collect and simulate field data on movement patterns.

The model should only be used in relatively uniform habitats such as cereal crops. This is because the probability of encountering each trap is supposed to be equal intraspecifically. This is likely to be the case in a regularly sown cereal crop since the resistance of the habitat to the movement of beetles is largely confined to the density of vertical plant stems which is approximately regular. Where the habitat surrounding each trap differs considerably, then this assumption will not be upheld.

The rate of avoidance of pitfall traps is likely to be more complex than is suggested by the results presented in Chapter 4. The tentative conclusion that avoidance is independent of activity rate within the same species was drawn from the results of only one species. This conflicts with the hypothesis presented in Section 4.4 that larger beetles are captured more readily than smaller beetles because of their greater relative velocity (i.e. that activity determines avoidance interspecifically). This was not proved conclusively and other interpretations are possible e.g. larger beetles tend to be nocturnal and may be less capable of perceiving and avoiding pitfall traps.

Vlijm *et al.* (1968) found that teneralis of *Calathus melanocephalus* were more susceptible to capture than mature adult beetles (i.e. the two groups were not captured in proportion to their abundance). Another possibility not tested in this study is that intraspecific variations in avoidance rates might exist with respect to the physiological state of individual beetles. Hayes (1970) found that different sizes and sexes of the oniscoid isopod *Tylos punctatus* were not captured in proportion to their abundance although it was not clear whether this was due to differences in activity (and therefore encounter rate) or differences in behaviour at the perimeter of the trap. An experiment described in Appendix 6 shows that when the rate of encounter is taken into account, the rate of avoidance of traps does not differ with respect to the sexes of the two

species studied.

The avoidance parameter is unlikely to remain constant temporally and deserves more detailed study. Whether the interspecific relationship between mean body length and avoidance rate will tolerate such refinements remains to be seen. It would be extremely useful if it did since the avoidance rate of new species could be predicted from their body length alone and experimental determination would not be necessary (as stressed above, the relationship is only likely to hold for species of similar body form (cf. Forsythe, 1987b). This was demonstrated in the present study for *Pterostichus angustatus*: close agreement was found between the predicted and actual avoidance rates (see Chapter 4 p.)).

The model will only be valid if the pitfall traps used to determine the rate of avoidance of each species are the same as those used to collect pitfall data in the field. It has been shown (Luff, 1975; Waage, 1985) that the type of trap used determines the number of individuals of a particular species captured. It is also necessary to keep the distance between adjacent traps constant, and this distance should be the same in the field grid and in the computer simulation of that grid. It is also important to attend to pitfall traps regularly so that the rim of the trap is kept flush with the surface of the soil. If this is not the case then the avoidance rate is unlikely to remain constant. Adis (1979) argues for an international standard pitfall trap to be used by all ecologists. This would allow parameters such as the avoidance rate to be used on all pitfall-trap data sets irrespective of the type of habitat since avoidance rate is independent of encounter rate (which can be determined by the habitat resistance to locomotor activity).

The degree of accuracy of the model presented in this thesis can only be determined if data on absolute abundance is available for the same period for which pitfall traps are in operation in the field. These values

are converted to relative abundances (P_A) for a group of species and the values compared with the relative abundances of the species as predicted by the model ($\hat{P}_{enc}$). Consequently, the population density estimates must be accurate. A method was used in this study to check the accuracy of quadrat data (Chapter 3) and other simple methods have been proposed (e.g. Brenoe (1987) suggests soaking the soil with water to bring individual beetles up to the surface and then extracting the remaining soil in the laboratory). It is more difficult to obtain valid estimates for large nocturnal species which cannot be easily studied using quadrats. The accuracy of mark-release-recapture models depends on the recapture rate and subsequent estimation of population density from population size is difficult when the exact surface area being sampled is unknown. Such a problem could be overcome by using enclosures and pitfall traps. The number of traps used could be increased where population density is low to overcome the problem of low recapture data.

As refinements are built into the model and its assumptions quantified, it should become more complex but hopefully more accurate. Once this is achieved, then an estimate of the absolute abundance, in terms of number of individuals m^{-2} , of only one species is required to determine the absolute abundance of all other species since the model is, in theory, capable of producing accurate estimates of relative population density.

I believe that in future years, the absolute abundance of species of Carabidae will be linked to the economic threshold of damage to crops by aphids. If this is achieved then the unnecessary application of pesticides, which, in the long run, are more detrimental to natural enemies of pests than to the pests themselves, could be avoided. A rapid and accurate technique which is low on manpower is necessary for estimates of absolute abundance of carabids to be made.

The accuracy of predictions of absolute population density from $\hat{P}_{cap}$ will be determined by the significance of the correlations between $\hat{P}_{cap}$ and P_A discussed on page 232. Ideally, predictions should only be accepted if the correlation coefficient is significant. The predictions were given in this thesis (Table 6.6) simply to show how predictions are ultimately made from pitfall-trap data and to show the magnitude of error at different levels of significance. If, after improvements and further testing, the model proves to be an accurate one, I would like to see it used to predict absolute abundance of aphidophagous Carabidae from pitfall-trap data. This will be of use if economic thresholds of aphid damage to cereal crops can be linked to the absolute abundance of their natural carabid predators. If the economic threshold, in terms of the number of aphids per tiller, is approached, then some rapid assessment as to whether it will be exceeded and whether such a situation can be prevented by the pest's natural enemies will be necessary if the application of chemicals is to be avoided. If pitfall traps are in constant operation in the crop then the predictive approach presented in this thesis seems suited to such a task.

I hope that the approach presented in the present study is followed up, ideally by a research team since in my opinion, the collection of adequate data (i.e. representing more individuals and species than in this study) for each of the parameters over a short period of time is not a task that can be achieved by one person. The arable field within Charnwood Lodge Nature Reserve was a useful study site because of the non-intensive management of the crops. In other situations where the diversity of the insect fauna has been reduced by systematic application of chemicals, the choice of species and abundance of individuals might not be as great. To test the predictive model thoroughly it will be necessary to study a wide range of species with respect to body length and for which data on absolute abundance can be readily collected.

SUMMARY

1. The estimation of population densities of carabid beetles in a cereal crop was attempted using a new technique.
2. Four sets of data were collected for this purpose:
 - i) Pitfall-trap data from the cereal crop.
 - ii) Data on activity patterns of individual beetles in the cereal crop.
 - iii) Data on the avoidance rate of pitfall traps in the laboratory.
 - iv) Data on the absolute abundance of beetles in the cereal crop.
3. Interspecific estimates of avoidance rate, velocity, actual distance and linear distance were all found to be dependent upon body length through regression analysis.
4. The movement of individuals of 5 species of Carabidae was simulated on a computer using data collected from the field. A census of each population was taken using hypothetical pitfall traps. The probability of an individual beetle encountering a trap in the field was estimated by equating it to the proportion of the population encountering traps in simulations.
5. The probability of encountering and the avoidance rate were used to modify pitfall-trap data for each species. This gave the estimated corrected number of individuals trapped, a hypothetical parameter.
6. This parameter was converted to a relative estimate of the abundance of species in pitfall traps and correlated with the relative abundance of the species in the field (from 2 iv above).
7. The data for August 1986, when species representing the greatest range of body lengths were studied, suggest that the correlation between the two relative estimates of abundance gives a higher correlation coefficient than when the actual (unmodified) relative abundances of species in pitfall traps (from 2 i above) are compared with relative abundance estimates from the field.
8. Ways in which the technique could be improved were discussed. It was suggested that, with refinements, it could be used to predict population

densities of carabids from pitfall-trap data and that this could be useful in Integrated Pest Management programs in the future.

Appendix 1

Species of Carabidae recorded from Charnwood Lodge Nature Reserve

<i>Carabus problematicus</i>	Herbst, 1786 s. <i>gallicus</i> Gehin, 1885	□
<i>C. violaceus</i>	Linnaeus, 1758	□
<i>C. monilis</i>	Fabricius, 1792	□
<i>C. nemoralis</i>	Müller, O. F., 1764	*
<i>Cychrus caraboides</i>	(Linnaeus, 1758) s. <i>rostratus</i> (Linnaeus, 1761)	□
<i>Leistus ferrugineus</i>	(Linnaeus, 1758)	□
<i>L. rufomarginatus</i>	(Duftschmid, 1812)	□
<i>Nebria brevicollis</i>	(Fabricius, 1792)	□
<i>N. salina</i>	Fairmaire & Laboulbène, 1856	⊙
<i>Notiophilus biguttatus</i>	(Fabricius, 1779)	*
<i>N. substriatus</i>	Waterhouse, G. R., 1833	⊙
<i>Elaphrus cupreus</i>	Duftschmid, 1812	□
<i>Loricera pilicornis</i>	(Fabricius, 1775)	*
<i>Clivina fossor</i>	(Linnaeus, 1758)	*
<i>Trechus quadristriatus</i>	(Schrank, 1781)	*
<i>T. secalis</i>	(Paykull, 1790)	⊙
<i>Asaphidion flavipes</i>	(Linnaeus, 1761)	*
<i>Bembidion aeneum</i>	Germar, 1824	*
<i>B. guttula</i>	(Fabricius, 1792)	*
<i>B. lampros</i>	(Herbst, 1784)	*
<i>B. lunulatum</i>	(Fourcroy, 1785)	*
<i>B. obtusum</i>	Serville, 1821	*
<i>B. quadrimaculatum</i>	(Linnaeus, 1761)	*
<i>B. tetracolum</i>	Say, 1823	*
<i>Pterostichus angustatus</i>	(Duftschmid, 1812)	□
<i>P. cupreus</i>	(Linnaeus, 1758)	*
<i>P. diligens</i>	(Sturm, 1824)	□
<i>P. madidus</i>	(Fabricius, 1775)	□
<i>P. melanarius</i>	(Illiger, 1798)	*
<i>P. niger</i>	(Schaller, 1783)	*
<i>P. strenuus</i>	(Panzer, 1796)	*
<i>Abax parallelepipedus</i>	(Piller & Mitterpacher, 1783)	□
<i>Calathus melanocephalus</i>	(Linnaeus, 1758)	□
<i>C. piceus</i>	(Marsham, 1802)	□
<i>Agonum dorsale</i>	(Pontoppidan, 1763)	*
<i>A. muelleri</i>	(Herbst, 1784)	*
<i>A. thoreyi</i>	Dejean, 1828	□
<i>Amara apricaria</i>	(Paykull, 1790)	⊙
<i>A. communis</i>	(Panzer, 1797)	□
<i>A. lunicollis</i>	Schödtte, 1837	□
<i>A. plebeja</i>	(Gyllenhal, 1810)	□
<i>A. similata</i>	(Gyllenhal, 1810)	⊙
<i>Harpalus latus</i>	(Linnaeus, 1758)	□
<i>H. rufipes</i>	(Degeer, 1774)	*
<i>Bradycellus harpalinus</i>	(Serville, 1821)	⊙
<i>B. ruficollis</i>	(Stephens, 1828)	⊙
<i>Badister unipustulatus</i>	Bonelli, 1813	⊙
<i>Dromius agilis</i>	(Fabricius, 1787)	□

* = species recorded from the arable study site April 1985 to August 1987.

⊙ = species recorded from the Reserve 1973 - 1984 but not during the present study.

□ = species recorded within the Reserve (from habitats other than the arable study site) October 1984 to August 1987.

Appendix 2

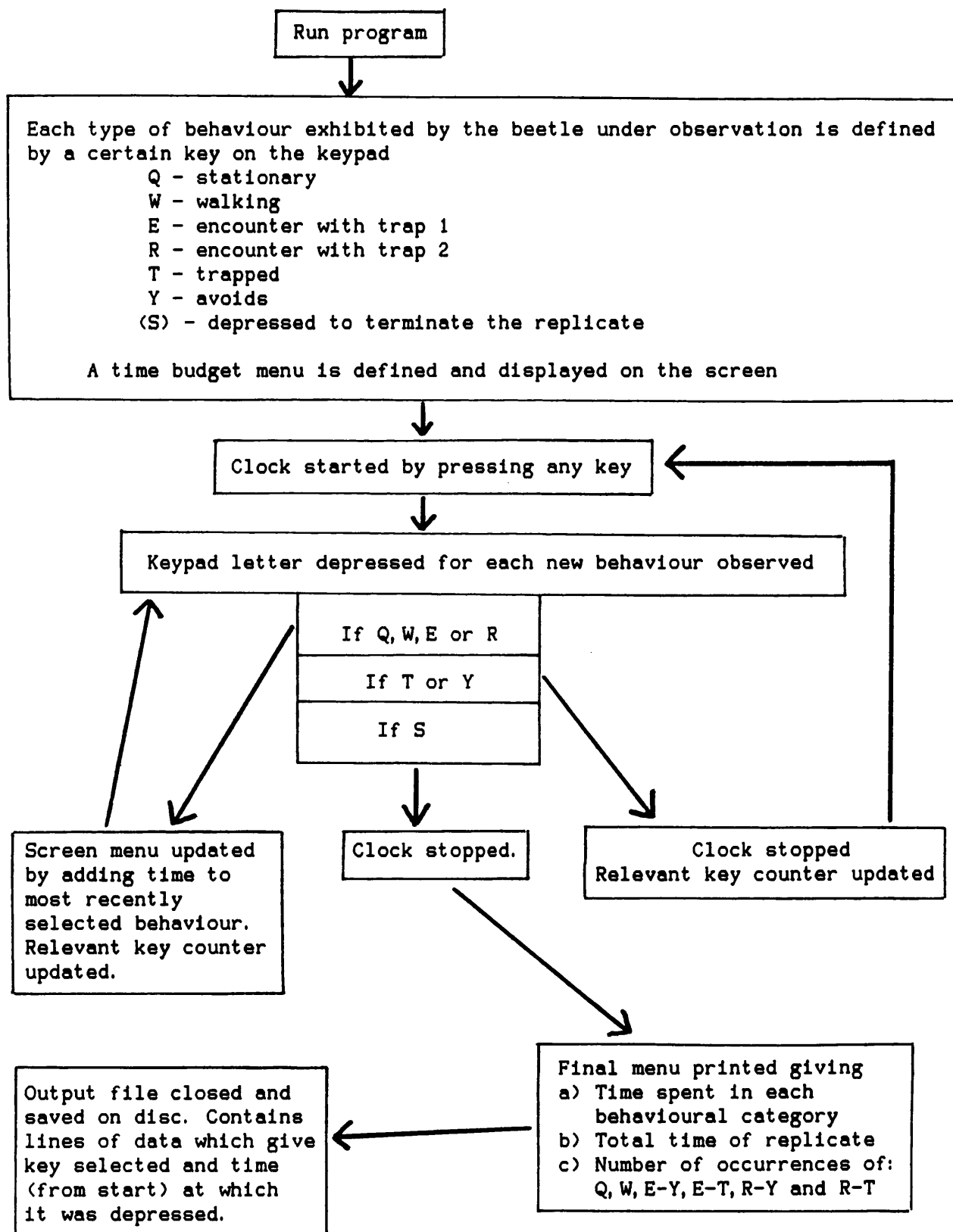
Details of equipment used during the study and referenced in the text

- i 225ml Perspex jar with screw thread and removable cap. A.R. Horwell Ltd.
Diameter at open end (distance between inner rim) = 5.5cm
Maximum diameter = 6.8cm
Diameter at base = 6.2cm
Height = 8.0cm
- ii White plastic drinking cup. Woolco.
Normal height = 8.7cm
Diameter at open end = 6.4cm
Diameter at open end when upper 4cm removed = 5.5cm
Diameter at base = 4.2cm
Circumference of trap = 17.3cm
- iii 700ml plastic pot with screw thread and removable top.
Height = 9cm
Diameter at open end (distance between inner rim) = 10cm
Diameter at base = 10cm
Circumference of trap = 31.4cm
- iv Grant Squirrell SQ 8 digital meter/logger model 1201 with two thermistor inputs and 8000 8-bit bytes of memory. 9V battery. Accurate to 0.2°C
- v Cassella copper rain gauge. Cat. no. W5366. C.F. Cassella Ltd., London, 1975.
- vi Red light. 1% transmission below 629nm.
5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 10cm distance (machine determined).
- vii Clear perspex cylinder.
Diam. of open ends (distance between inner surface) = 15cm
Height = 15cm
Height above soil = 13cm
Thickness of perspex = 0.5cm
- viii Timex water-resistant stop watch accurate to 0.01 seconds and capable of emitting an alarm at desired time intervals
- ix White plastic gardener's stake/peg. Nottcutt's Ltd.
15cm $\times$ 2cm $\times$ 0.2cm with tapered end.
- x 'Silva' Type 3 compass, 1 degree scale.

Appendix 3

BASIC program "Beetle" suitable for BBC model B microcomputer

A 3.1 Flow chart showing main features of "Beetle".



A 3.2 BASIC program "Beetle"

```
10 REM          B E E T L E
20 REM          =====
30
40 REM  TO MONITOR BEHAVIOUR OF A
50 REM  BEETLE IN AN ARENA WITH 2 TRAPS
60
70
80
90 REM *****
100 REM *                                     *
110 REM *  WRITTEN BY PETER HAYHURST          *
120 REM *  (LEICESTER UNIVERSITY COMPUTER CENTRE) *
130 REM *  AND DAVID LEWIS                    *
140 REM *  (LEICESTER UNIVERSITY ZOOLOGY DEPT.) *
150 REM *  MARCH 1986                        *
160 REM *                                     *
170 REM *****
180
190
200
210 CLS
220 PRINT TAB (10,3) ; "BEETLE"
230 PRINT TAB (10,4) ; "====="
240 REM CLEAR THE PREVIOUS COMMAND COUNTERS
250 LAST=0
260 PREV=0
270 REM CLAEER THE OUTPUT CHANNEL NUMBER
280 NAMF=0
290 REM ZERO THE EVENT TIMERS
300 TQ=0
310 TU=0
320 TE=0
330 TR=0
340 REM ZERO THE TIME COUNTER
350 NOW=0
360 REM CLEAR THE KEY CODE VARIABLE
370 N=0
380 REM CLEAR THE EVENT COUNTERS
390 NQ=0
400 NU=0
410 NE=0
420 NR=0
430 NT=0
440 NA=0
450 NY=0
460 NS=0
470 REM CLEAR THE TIME VARIABLES
480 MIN=0
490 SEC=0
500 REM CLEAR THE MOST RECENT KEY STORE
510 STAT$=" "
520 REM CLEAR THE SEQUENCE COUNTERS
530 NET=0
540 NEY=0
550 NRT=0
560 NRY=0
570 NQAU=0
```

```

580 NQAQ=0
590 NUAU=0
600 NUAQ=0
610 REM OPEN THE DISC OUTPUT FILE
620 PRINT TAB(1,6); "PLEASE ENTER DISC FILE NAME"
630 PRINT TAB(1,7);
640 INPUT NAMES$
650 NAMF=OPENOUT(NAMES$)
660 PRINT TAB(1,9); "PLEASE ENTER COMMENT LINE"
670 PRINT TAB(1,10);
680 INPUT COM$
690 REM FILE COMMENT WITH DATA FILE
700 PRINT$ NAMF, "COMMENT - "+COM$
710 PRINT TAB(1,20); "PRESS ANY KEY TO START"
720 X=GET
730 REM FILE INITIAL TIME
740 PRINT$ NAMF, STAT$+" "+STR$(NOW)
750 TIME=0
760 REM CLEAR THE SCREEN AND START
770 CLS
780 REM INITIALISE THE SCREEN
790 PROSCREEN
800 REM CALCULATE THE CURRENT TIME
810 OLD=NOW
820 NOW=TIME
830 SEC=(NOW DIV 100)MOD 60
840 MIN=(NOW DIV 6000)MOD 60
850 REM READ IN KEY
860 NOLD=N
870 REM DECIDE IF ITS A NEW KEY
880 M=INKEY(0)
890 IF M=-1 THEN GOTO 1030
900 IF M=81 THEN GOTO 990
910 IF M=85 THEN GOTO 990
920 IF M=69 THEN GOTO 990
930 IF M=82 THEN GOTO 990
940 IF M=84 THEN GOTO 990
950 IF M=89 THEN GOTO 990
960 IF M=65 THEN GOTO 990
970 IF M=83 THEN GOTO 990
980 GOTO 1030
990 PREV=LAST
1000 LAST=N
1010 N=M
1020 REM TAKE ACTION ON KEY
1030 IF N=81 THEN PROCQ
1040 IF N=85 THEN PROCU
1050 IF N=69 THEN PROCE
1060 IF N=82 THEN PROCR
1070 IF N=84 THEN PROCT
1080 IF N=89 THEN PROCY
1090 IF N=65 THEN PROCA
1100 IF N=83 THEN PROCS
1110 REM UPDATE THE SCREEN
1120 PROCUPDATE
1130 REM SEE IF TIME IS FINISHED
1140 IF NOW>360000 THEN GOTO 1180
1150 REM SEE IF THE TEST HAS BEEN STOPPED
1160 IF STAT$<>"S" THEN GOTO 810
1170 REM PRINT OUT THE COUNTER TOTALS

```

```

1180 PRINT TAB(3,17); "SEQUENCES"
1190 PRINT TAB(3,19); "ET "; NET
1200 PRINT TAB(3,20); "EY "; NEY
1210 PRINT TAB(3,21); "RT "; NRT
1220 PRINT TAB(3,22); "RY "; NRY
1230 PRINT TAB(20,19); "QAU "; NQAU
1240 PRINT TAB(20,20); "QAA "; NQAA
1250 PRINT TAB(20,21); "UAU "; NUAU
1260 PRINT TAB(20,22); "UAQ "; NUAQ
1270 REM CLOSE THE DATA OUTPUT FILE
1280 CLOSE# NAMF
1290 REM SEE IF THAT WAS THE LAST EXPERIMENT
1300 PRINT TAB(1,24); "PRESS-(F)INISH, (P)RINT, OR (C)ONTINUE"
1310 X=GET
1320 IF X<>80 THEN GOTO 1360
1330 PROCPOUT
1340 PRINT " PRESS F TO FINISH, ELSE CONTINUE"
1350 X=GET
1360 IF X<>70 THEN GOTO 10
1370 CLS
1380 STOP
1390
1400
1410
1420 DEF PROSCREEN
1430 REM INITIALISE THE SCREEN
1440 CLS
1450 PRINT TAB(1,1); "BEETLE"
1460 PRINT TAB(1,2); "====="
1470 PRINT TAB(1,4); "LAST KEY ( )"
1480 PRINT TAB(20,1); "TIME SO FAR"
1490 PRINT TAB(20,2); "====="
1500 PRINT TAB(3,6); "KEY ACTIVITY   TIMES TIME(SEC)"
1510 PRINT TAB(3,8); "Q   STATIONARY"
1520 PRINT TAB(3,9); "U   WALKING"
1530 PRINT TAB(3,10); "E   TRAP1"
1540 PRINT TAB(3,11); "R   TRAP2"
1550 PRINT TAB(3,12); "T   TRAPPED"
1560 PRINT TAB(3,13); "Y   AVOID"
1570 PRINT TAB(3,14); "A   ENCOUNTER
1580 PPRINT TAB(3,15); "S STOP"
1590
1600
1610
1620 DEF PROCUPATE
1630 REM PUT THE CURRENT COUNTER TOTALS ON THE SCREEN
1640 REM DISPLAY TIME IN BOTH MIN: SEC AND SEC
1650 PRINT TAB(20,4); MIN; ": "; SEC; " "
1660 PRINT TAB(30,4); " ("; INT(NOW/100); ")"
1670 PRINT TAB(11,4); STAT$
1680 PRINT TAB(19,8); NQ
1690 PRINT TAB(19,9); NU
1700 PRINT TAB(19,10); NE
1710 PRINT TAB(19,11); NR
1720 PRINT TAB(19,12); NT
1730 PRINT TAB(19,13); NY
1740 PRINT TAB(19,14); NA
1750 PRINT TAB(19,15); NS
1760 REM DISPLAY THE TIMERS IN SEC ONLY
1770 PRINT TAB(25,8); INT(TQ/100)

```

```

1780 PRINT TAB(25, 9); INT(TU/100)
1790 PRINT TAB(25, 10); INT(TE/100)
1800 PRINT TAB(25, 11); INT(TR/100)
1810 ENDPROC
1820 DEF PROCPOUT
1830 REM TO PRINT OUT THE SCREEN RESULTS
1840 CLS
1845 *FX6, 0
1850 VDU2
1860 PRINT
1870 PRINT "DATA FILE ", NAME$
1880 PRINT "COMMENT ", COM$
1890 PRINT
1900 PRINT "TIME      ", MIN; ": "; SEC, NOW/100; " (SEC)"
1910 PRINT
1920 PRINT "STATIONARY  ", NQ, TQ/100; " (SEC)"
1930 PRINT "WALKING      ", NU, TU/100; " (SEC)"
1940 PRINT "TRAP1        ", NE, TE/100; " (SEC)"
1950 PRINT "TRAP2        ", NR, TR/100; " (SEC)"
1960 PRINT "TRAPPED       ", NT
1970 PRINT "AVOIDED        ", NY
1980 PRINT "ENCOUNTER     ", NA
1990 PRINT "STOPPED       ", NS
2000 PRINT
2010 PRINT "SEQUENCES"
2020 PRINT
2030 PRINT "ET "; NET
2040 PRINT "EY "; NEY
2050 PRINT "RT "; NRT
2060 PRINT "RY "; NRY
2070 PRINT "QAU "; NQAU
2080 PRINT "QAQ "; NQAQ
2090 PRINT "UAU "; NUAU
2100 PRINT "UAQ "; NUAQ
2110 PRINT
2120 VDU3
2430 ENDPROC
2140
2150
2160
2170 REM *****
2180 REM * *
2190 REM * KEY SERVERS *
2200 REM * *
2210 REM *****
2220
2230
2240
2250 DEF PROCQ
2260 IF NOLD=N THEN GOTO 2330
2270 PRINT$ NAME, "Q "+STR$(NOW)
2280 IF LAST<>65 THEN GOTO 2310
2290 IF PREV=81 THEN NQAQ=NQAQ+1
2300 IF PREV=85 THEN NUAQ=NUAQ+1
2310 NQ=NQ+1
2320 STAT$="Q"
2330 TQ=TQ+(NOW-OLDT)
2340 ENDPROC
2350
2360

```

```

2370
2380 DEF PROCU
2390 IF NOLD=N THEN GOTO 2460
2400 PRINT£ NAMF, "U "+STR$(NOW)
2410 IF LAST<>65 THEN GOTO 2440
2420 IF PREV=81 THEN NQAU=NQAU+1
2430 IF PREV=85 THEN NUAU=NUAU+1
2440 STAT$="U"
2450 NU=NU+1
2460 TU=TU+(NOW-OLDT)
2470 ENDPROC
2480
2490
2500
2510 DEF PROCE
2520 IF NOLD=N THEN GOTO 2560
2530 PRINT£ NAMF, "E "+STR$(NOW)
2540 STAT$="E"
2550 NE=NE+1
2560 TE=TE+(NOW-OLDT)
2570 ENDPROC
2580
2590
2600
2610 DEF PROCR
2620 IF NOLD=N THEN GOTO 2660
2630 PRINT NAMF, "R "+STR$(NOW)
2640 NR=NR+1
2650 STAT$="R"
2660 TR=TR+(NOW-OLDT)
2670 ENDPROC
2680
2690
2700
2710 DEF PROCT
2720 IF N=NOLD THEN GOTO 2770
2730 PRINT£ NAMF, "T "+STR$(NOW)
2740 NT=NT+1
2750 IF LAST=69 THEN NET=NET+1
2760 IF LAST=82 THEN NRT=NRT+1
2770 STAT$="T"
2780 PRINT TAB(3, 20); "PRESS ANY KEY"
2790 X=GET
2800 PRINT TAB(3, 20); "
2810 TIME=NOW
2820 NOLD=0
2830 STAT$="T"
2840 M=X
2850 GOTO 890
2860 ENDPROC
2870
2880
2890
2900 DEF PROCY
2910 IF N=NOLD THEN GOTO 2960
2920 PRINT£ NAMF, "Y "+STR$(NOW)
2930 NY=NY+1
2940 IF LAST=69 THEN NEY=NEY+1
2950 IF LAST=82 THEN NRY=NRY+1
2960 STAT$="Y"

```

```
2970 PRINT TAB(3,20);"PRESS U TO CONTINUE"
2980 M=GET
2990 IF M<>85 THEN GOTO 2980
3000 PRINT TAB(3,20);"
3010 TIME=NOW
3020 NOLD=0
3030 GOTO 890
3040 ENDPROC
3050
3060
3070
3080 DEF PROCA
3090 IF NOLD=N THEN GOTO 3120
3100 PRINT$ NAMF,"A "STR$(NOW)
3110 NA=NA+1
3120 STAT$="A"
3130 ENDPROC
3140
3150
3160
3170 DEF PROCS
3180 PRINT$ NAMF,"S "+STR$(NOW)
3190 IF NOLD<>N THEN NS=NS+1
3200 STAT$="S"
3210 ENDPROC
```


FORTTRAN Simulation Program

```
C
C Written by David Lewis, Dept. of Zoology, Univ. of Leicester
C
C Before each run set the parameters
C
C ISEED - random number generator
C NUMREL - number of beetles to be released onto grid
C TIME - individual replicates: 1 unit = 15 mins
C                               48 units = 12 hrs
C                               336 units = 1 week
C PROPn - relative proportion of each species
C           (from data on absolute population density)
C RADIUS - radius of the trap in m
C SPACING - distance between traps within a row and between rows
C
C COMMON J1(510),J2(510),B1(510),I2(510)
C
C J1=species code J2=individual code
C B1=distance moved since last position (mm)
C I2=bearing to next position (degrees)
C
C SP1=N.biguttatus, SP2=P.melanarius, SP3=B.quadrimaculatum
C SP4=B.lampros SP5=A.muelleri
C
C INTEGER TIME, RELEASE, RELSP1, RELSP2, RELSP3, RELSP4, RELSP5,
C *ANGLE(34), SPK
C REAL MOVENO, NUMREL
CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C
C PARAMETER (RADIUS=0.0275, SPACING=5)
C PARAMETER (NUMREL=5040)
C PARAMETER (TIME=672)
C PARAMETER (PROP1=0.2)
C PARAMETER (PROP2=0.2)
C PARAMETER (PROP3=0.2)
C PARAMETER (PROP4=0.2)
C PARAMETER (PROP5=0.2)
C
CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C
C OPEN (2, FILE='[DWL.AC86]ACF.DAT', STATUS='OLD')
C OPEN (3, FILE='[DWL.SIM]SIM.DAT', STATUS='NEW')
C DATA ANGLE/52, 59, 81, 97, 112, 96, 64, 57, 66, 68, 56, 53,
C *61, 79, 60, 58, 52, 43, 65, 102, 58, 5, 23, 23, 81, 69, 61, 44, 58, 35,
C *111, 96, 80, 103/
C ISEED=76541
C IA=-14
C IB=0
C LNO=0
C
C read in the data
C
```

```

DO L+1,510
READ (2,200)J1(L),J3(L),B1(L),I2(L)
ENDDO

C
C Calculate how many times each individual is released.
C In the data file ACF.DAT individuals of the 5 species
C occur in the ratio 9:9:6:6:4
C
C
RELSP1=NINT(PROP1*NUMREL/9)
RELSP2=NINT(PROP2*NUMREL/9)
RELSP3=NINT(PROP3*NUMREL/6)
RELSP4=NINT(PROP4*NUMREL/6)
RELSP5=NINT(PROP5*NUMREL/4)

C
C First loop: One individual per loop. There are 15 lines of data per
C individual
C
DO 7 K1=1,34
IA=IA+15
IB=IB+15
IF (IA.LT.136) THEN
RELEASE=RELSP1
SPK=9
ELSE IF (IA.LT.271.AND. IA.GT.135) THEN
RELEASE=RELSP2
SPK=9
ELSE IF (IA.LT.361.AND. IA.GT.270) THEN
RELEASE=RELSP3
SPK=6
ELSE IF (IA.LT.451.AND. IA.GT.360) THEN
RELEASE=RELSP4
SPK=6
ELSE IF (IA.LT.511.AND. IA.GT.450) THEN
RELEASE=RELSP5
SPK=4
ENDIF
IF (RELEASE.EQ.0) GOTO 7

C
C
C Second loop: Individual replicates with random start position.
C If population density (PROPn) = 0 then no beetles released.
C Beetles released a number of times according to relative density
C
C
DO 8 K2=1,RELEASE
ICOUNT=1
ITCOUNT=0
ITRAP=0
IAVOID=0
MOVENO=0

C
C Random starting angle for each release
C
C=360*RAN(ISEED)
X=500.5
Y=500.5

C
C Third loop: Number of repeats of the data set (15 lines)
C

```

```

DO 77 K3=1, TIME
C
C
C Fourth loop: The individual moves representing 1 minute each.
C Each move calls the subroutine to determine whether the beetle
C has encountered a trap.
C
C FM=0
DO 777 K4=IA, IB
FM=FM+1
MOVENO=MOVENO+1
IF (ITRAP.EQ. 1. OR. ICOUNT.EQ. 1) THEN
X=500.5
Y=500.5
MOVENO=1
FM=1
ICOUNT=1
ITRAP=0
C=360*RAN(ISEED)
ENDIF
IF (FM.EQ. 1. AND. ICOUNT.NE. 1) THEN
P1=RAN(ISEED)
IF (P1.LE. 0.5) P=-1
IF (P1.GT. 0.5) P=1
C=C+(ANGLE(K1)*P)
ENDIF
CALL CAPTURE (C, ITRAP, IAVOID, ICOUNT, K2, X, Y,
*FM, MOVENO, RADIUS, SPACING)
ICOUNT=0
IF (ITRAP.EQ. 1) ITCOUNT=ITCOUNT+1
777 CONTINUE
77 CONTINUE
LNO=LNO+1
IF (ITCOUNT.GT. 0) GOTO 2
GOTO 3
C
C Beetle was trapped
C
2 WRITE (3, 300) LNO, J1(K4-1), J2(K4-1), ITCOUNT, IAVOID, MOVENO,
* ((MOVENO/(TIME*15))*100, RELEASE*SPK
GOTO 8
C
C Beetle was not trapped
C
3 WRITE (3, 300) LNO, J1(K4-1), J2(K4-1), ITCOUNT, IAVOID, MOVENO,
* ((MOVENO/(TIME*15))*100, RELEASE*SPK
C
C Release the same individual again unless REPEATS=max
C
8 CONTINUE
C
C Release another individual
C
7 CONTINUE
200 FORMAT (8X, I4, 15X, I2, 9X, F4.0, 4X, I4)
300 FORMAT (X, I6, X, I4, 3(X, I2), X, F7.0, X, F6.2, X, I6)
STOP
END
C
C

```

```

C
CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C
C
C          S U B R O U T I N E
C
C
C
CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C
C
SUBROUTINE CAPTURE (C, ITRAP, IAVOID, ICOUNT, K2, X, Y,
*FM, MOVENO, RADIUS, SPACING)
COMMON (J1(510), J2(510), B1(510), I2(510))
IF (FM. EQ. 1. OR. ICOUNT. EQ. 1) GOTO 1
GOTO 2

C
C
C    All moves are in mm. Convert to metres: B1/1000.
C    Divide by the distance between traps (B1/SPACING) since the
C    hypothetical grid defined below has traps spaced at 1m intervals
C
C    C is a random angle when:
C
C    a) On the very first move
C    b) If the beetle has just been trapped
C    c) If the beetle has been relocated
C
C    On subsequent first moves/data set (each repeat of the TIME loop)
C    the mean deviation per move (ANGLE) is used for C
C
1 X=X+(SIN(C)*(B1(K4)/(1000*SPACING)))
Y=Y+(COS(C)*(B1(K4)/(1000*SPACING)))
GOTO 3

C
C    Read in the new angle which is on the data line before
C    the current line. The distance moved since last position
C    is on the current data line.
C
2 C=C+I2(K4-1)
IF (C. GT. 360)C=C-360
IF (C. LT. -360)C=C+360
X=X+(SIN(C)*(B1(K4)/(1000*SPACING)))
Y=Y+(COS(C)*(B1(K4)/(1000*SPACING)))
IF (X. LT. 0. OR. X. GT. 1000. OR. Y. LT. 0. OR. Y. GT. 1000) THEN
X=500.5
Y=500.5
ENDIF

C
C    XN set to nearest integer of X
C    YN set to nearest integer of Y
C
3 XN=ANINT(X)
YN=ANINT(Y)

C
C    All values made equivalent on a scale of 0 to 1
C    by removing negative signs
C
DX=ABS(X-XN)
DY=ABS(Y-YN)

```

```

C      Let DXY be the radius of the trap
C
C      DXY=SQRT(DX**2+DY**2)
C
C      Beetle is trapped if its position is less than the critical
C      value, which can be altered according to the size of the trap
C      used. This radius must be altered according to the trap spacing
C      i. e. the scale of the grid.
C
C      IF (DXY.LE. (RADIUS/SPACING))GOTO 4
C      GOTO 5
4 P=RAN(ISEED)
C
C      Avoidance parameter is taken into account
C
C      IF (J1(K4).EQ.6603.AND. P.GT.0.8867) THEN
C      ITRAP=1
C      ELSE IF (J1(K4).EQ.8315.AND. P.GT.0.1606) THEN
C      ITRAP=1
C      ELSE IF (J1(K4).EQ.1344.AND. P.GT.0.6306) THEN
C      ITRAP=1
C      ELSE IF (J1(K4).EQ.1325.AND. P.GT.0.8023) THEN
C      ITRAP=1
C      ELSE IF (J1(K4).EQ.0611.AND. P.GT.0.8) THEN
C      ITRAP=1
C      ELSE
C
C      Beetle is relocated after avoiding
C
C      Y=((Y-0.353)/SPACING)
C      X=((X-0.353)/SPACING)
C      IAVOID=IAVOID+1
C      ENDIF
5 CONTINUE
C
C      One move completed, return to main program
C
C      RETURN
C      END

```

Appendix 5

Experiment to determine the effect of metal covers on pitfall trap captures

Introduction

The pitfall traps in operation at Charnwood Lodge prior to the commencement of this research utilised aluminium covers to prevent traps becoming flooded during heavy rainfall, to prevent predation of the trap contents by mammals and birds and to minimise the quantity of leaf litter, soil and other debris falling into the trap.

It was thought that such covers might influence the behaviour of individual beetles in a non-uniform way with respect to different species. Other features of pitfall traps are already known to do this: formaldehyde as a toxic preservative (Luff, 1968 and others), the size and composition of the trap (Luff, 1975) and the extent to which the area surrounding the trap is cleared of vegetation (Greenslade, 1964).

To determine whether non-transparent covers have an effect, it was decided to place a grid of pitfall traps in the study field half of which would be covered and the other half be the uncovered controls.

Material & Methods

A grid of 12 small pitfall traps (Appendix 2 [i and ii]) was operated adjacent to the main sampling grid between 23rd May and 7th July, 1985. The distance between traps and between rows was 5m. The grid was arranged in two rows of six so that alternate traps were covered. 6 traps were covered with aluminium squares (15cm × 15cm) raised on legs so that the horizontal surface of the metal which forms the cover was approximately 3cm above the soil surface and the rim of the trap. The legs were sunk into the soil to a depth of 2cm. The other 6 traps did not have

aluminium covers and were covered with chicken wire as described in Chapter 2. All traps contained 50ml of 50% (pbv) ethane diol and were emptied at least every 14 days and the number of individuals of each species of Carabidae recorded.

Results

A total of 372 beetles of 12 species was captured during the experiment; 175 in covered traps and 197 in uncovered traps. There is no significant difference between these two frequencies when the Chi squared test is applied to the null hypothesis. However, the main aim of the experiment was to analyse results intraspecifically. This is done using the Chi squared test in Table A5.1. The traps have been grouped into two groups of 6 and the total number of beetles summed for each category. This was possible because no traps were disturbed during the experiment and so the number of trap days was equal for each category. The expected frequency of beetles in each group of traps is taken to be the mean of the two observed frequencies.

A significant difference between the frequencies of individuals in each group of traps is revealed for 6 species. Two of these species occurred at higher than expected frequencies in covered traps: *Pterostichus strenuus* and *Notiophilus biguttatus*. The other four species were caught at higher than expected frequencies in uncovered traps. All four of these species were classed as diurnal at Charnwood (see Chapter 3). If all diurnal species are grouped together then the difference between the frequencies at which beetles occur in the two types of trap is significant too. However, when the data from the three nocturnal species is pooled then the opposite is not true: nocturnal species as a group did not occur at a significantly higher frequency in covered traps (*Nebria brevicollis*, although not studied with respect to diel periodicity at Charnwood, is a nocturnal species (Tipton, 1960; Penney, 1965)).

The species which revealed no significant difference in frequency were mainly represented by very few individuals but it is clear that *P. melanarius* shows no preference to either type of trap.

If the *Bembidini* are considered alone then the significance of the diurnal species bias in uncovered traps is increased. This is because the other diurnal species, *Notiophilus biguttatus* shows a significant bias towards covered traps.

Discussion

The data presented in Table A5.1 clearly show that certain species of Carabidae are captured more readily by covered traps than by uncovered traps and that for other species the opposite is true. It is not known whether this difference is due to an altered avoidance rate because of the presence of the metal cover or to an altered rate of encounter with covered traps. There is some suggestion in the results that diurnal species are captured less readily by covered traps. It might be expected that if the encounter rate with both groups of traps was equal, then diurnal species would be more readily captured by covered traps because they are less easy to see. This is clearly not the case and a more likely explanation would be that individuals of diurnal species avoid moving under the metal covers because of the increased risk of predation (small cracks and holes in the soil provide safer shelter (Pauer, 1975)). This would result in a lower than expected encounter rate with covered traps and hence fewer beetles would be captured.

Notiophilus biguttatus is a diurnal species the data for which refutes the above hypothesis. It has an unusual hunting strategy (Bauer, 1979) feeding mainly on Collembola. Collembola require humid conditions and may be more likely to occur under the metal covers than in the vicinity of open traps. Bauer et al. (1977) have demonstrated that brightness is essential for hunting success in this species. From 1 to 500lux hunting success

Table A5.1

Species	Periodicity	No. indiv. in covered traps	No. indiv. in uncovered traps	Chi Squared	p
<i>Agonum muelleri</i>	P	33	22	2.20	N.S.
<i>Loricera pilicornis</i>	P	5	14	4.26	*
<i>Nebria brevicollis</i>	N	3	3	0.00	N.S.
<i>Pterostichus melanarius</i>	N	52	70	2.66	N.S.
<i>P. strenuus</i>	N	33	9	13.71	***
<i>Notiophilus biguttatus</i>	D	17	5	6.55	*
<i>Bembidion lampros</i>	D	9	26	8.21	**
<i>B. guttula</i>	D	8	14	1.64	N.S.
<i>B. tetracolum</i>	D	4	6	0.40	N.S.
<i>B. obtusum</i>	D	2	1	0.33	N.S.
<i>B. quadrimaculatum</i>	D	3	11	4.57	*
<i>B. lunulatum</i>	D	6	16	4.55	*
Plastic		38	36	0.05	N.S.
Nocturnal		88	82	0.21	N.S.
Diurnal		49	79	7.03	**
<i>Bembidiini</i>		32	74	16.64	***

P=plastic N=nocturnal D=diurnal

p=probability that the null hypothesis is true

* = $0.01 < p < 0.05$ ** = $0.001 < p < 0.001$ *** = $p < 0.001$

N.S. = not significant ($p > 0.05$)

increases with increasing brightness. However, individual beetles probably have to reach a compromise between brightness and darker more humid microhabitats which are likely to be frequented by Collembola.

Of the three nocturnal species represented in pitfall traps, only two were caught in sufficient numbers to allow conclusions to be drawn. Individuals of *Pterostichus strenuus* are more readily captured in covered traps but *P. melanarius* shows no significant preference for either type of trap.

In the arable field at Charnwood there was an unusually high density of large stones on the soil surface (as stated in Chapter 2 the field is poorly managed). These would represent a source of cover for nocturnal beetles during the hours of daylight. In other, more intensively managed fields, such cover might be at a premium due to the removal of such stones and nocturnal beetles might take shelter under pitfall-trap covers at dawn more readily than they might at Charnwood.

The use of covers clearly introduces another complex parameter in to the equation since the response of beetles to their presence differs interspecifically in an apparently unpredictable way. If, when using pitfall traps in arable fields, the aim is to determine relative population density from modifying pitfall data, then it is suggested that the use of uncovered traps is the more suitable option. The trap contents can be protected by a wire cover, and drainage holes made in the sides of the inner plastic cup to prevent flooding of the trap during heavy rainfall.

Finally, the quantification of avoidance behaviour is much easier in both the laboratory and field when uncovered traps are used since the rim of the trap can be readily observed and access to the trap contents easily achieved.

Appendix 6

Further investigations into the causes of pitfall trap avoidance.

Introduction

Experiments 1 and 2 in Chapter 4 determined the rate of avoidance of 10 species of Carabidae. These rates were based on single encounters with pitfall traps by individual beetles. Conspecific beetles clearly differed in their response to the trap since some were captured and some avoided the trap. It was tentatively suggested that the response of individual beetles was independent of activity prior to the encounter.

Some workers have demonstrated that beetles (Vlijm *et al.*, 1968) or other arthropods (Hayes, 1970) differ intraspecifically in their susceptibility to capture by pitfall traps - their results are based on the fact that individuals of a particular sex or age are not captured in pitfall traps in the field in proportion to their abundance as determined by other methods. It should be pointed out that an alternative interpretation of such results is that the encounter rate of different sexes or other subgroups might not be equal or that individuals differ in their ability to escape from a trap once captured. The importance of taking into account the encounter rate was stressed in Chapter 4 and this is done in some of the investigations presented below.

Sex and avoidance

Male and female carabids often differ with respect to external structure. Males often have bristles on the anterior tarsi and might be more capable of resisting capture by pitfall traps as a consequence. The hypothesis that males and females of a particular species exhibit the same avoidance rate was tested in two ways:

1. By comparing the frequency at which the two sexes occur in pitfall traps in the field with their frequency in quadrat samples collected over the same

period. This method assumes that beetles of both sexes have an equal probability of encountering pitfall traps in the field.

2. By comparing the frequency of avoidance of the two sexes in the laboratory. This method takes into account the rate at which the two sexes encounter pitfall traps.

Damaged antennae and avoidance

It became apparent during the study that several beetles collected from the field, either by pitfall trapping or by pooter, had damaged antennae i.e. several antennal segments missing on one or both antennae. Observations of beetles encountering pitfall traps suggest that the head usually encounters the trap first. If the antennae are used to detect objects in the path of a beetle it seemed possible that damaged antennae would be less capable detectors than undamaged ones. The hypothesis that the rate of avoidance is unaffected by the state of the antennae was tested in two ways:

1. By comparing the frequency of beetles with damaged antennae in pitfall trap samples from the field with the frequency in quadrat samples collected over the same period. This method assumes that beetles with damaged antennae have an equal probability of encountering pitfall traps as do beetles with complete antennae.

2. By comparing the frequency of beetles with damaged antennae which were known to have avoided pitfall traps with the frequency of those which were known to have been captured. This method takes into account the rate of encounter with pitfall traps of the two groups.

Ratio of antennal length: body length and avoidance

It was considered possible that the length of antennae of beetles might be important in determining the rate of avoidance - relatively long antennae might be more capable of detecting pitfall traps and thus preventing the beetle being captured. The ratio of the length of one antenna to the total body length seemed a suitable parameter and a mean value was determined for several species. Regression of avoidance rate (suitably transformed) upon this ratio would reveal whether the hypothesis outlined above was a realistic one.

Material and Methods

Individuals of *Bembidion lampros* and *B. quadrimaculatum* were studied with respect to sex and antennal damage. Beetles captured by pitfall traps in the main sampling grid or collected from quadrats by pooter between 6th May and 30th June were preserved in 70% ethanol. At a later date they were sexed and the antennae examined under high magnification. If the full complement of 22 antennal segments were not present then the beetle was regarded as having damaged antennae.

Some of the beetles which had encountered pitfall traps in the laboratory (experiment 2; Chapter 4) were isolated in tubes containing 70% ethanol according to the type of response exhibited. All beetles had been collected by pooter in the field. The beetles were also sexed and examined with respect to antennal damage.

Beetles of 8 species were used to determine the ratio of the length of 1 antenna to body length. Antennae were dissected from heads and straightened in glycerol before measuring. The length was the distance from the base of the first segment to the apex of the 11th segment. Body length was determined as outlined in Chapter 2.

More beetles were examined with respect to antennal damage than were sexed

due to the relative speed at which results could be achieved.

All results were analysed using the Chi squared test but the calculation of expected frequencies differed according to the method (see results tables).

Results

1. Sex

32 individuals of each species captured in pitfall traps and 97 individuals of each species collected by pooter were sexed. All beetles were captured between 6th May and 3rd June 1987 and no attempt has been made to subdivide the data. No significant difference was found between the ratio of males:females with respect to the method of collection (Table A6.1). This suggests that males and females of each species were captured in proportion to their relative abundance in the field i.e. that sex has no effect on the rate of avoidance of pitfall traps. However, this conclusion is based on the assumption that individuals of both sexes have an equal probability of encountering pitfall traps in the field.

Table A6.1

Species	A Observed Frequency ♂ in Pitfalls	B Observed Frequency ♀ in Pitfalls	C Observed Frequency ♂ in Quadrats	D Observed Frequency ♀ in Quadrats	E Expected Frequency ♂ in Pitfalls	F Expected Frequency ♀ in Pitfalls	Chi Square	p
<i>B. lampros</i>	11	21	41	56	13.53	18.47	0.820	N.S.
<i>B. quad.</i>	15	17	48	49	15.83	16.16	0.087	N.S.

$$E = (A+B) \times C / (C+D) \quad F = (A+B) \times D / (C+D)$$

p = probability that different sexes occur in pitfall traps at equal frequencies

N.S. = $p > 0.05$

Although the second method of determining whether sex determines the rate of avoidance is more direct (it takes into account the rate of encounter of the two sexes) the data is more sparse (Table A6.2). No significant difference in avoidance rate was found between the two sexes.

Table A6.2

Species	A Observed Frequency ♂ Avoidance	B Observed Frequency ♂ Encounters	C Observed Frequency ♀ Avoidance	D Observed Frequency ♀ Encounters	E Expected Frequency ♂ Avoidance	F Expected Frequency ♀ Avoidance	Chi Square	p
B. lanpros	17	25	16	22	17.55	15.45	0.037	N.S.
B. quad.	14	28	22	30	17.38	18.62	1.271	N.S.

$$E = (A+C) \times B / (B+D) \quad F = (A+C) \times D / (B+D)$$

p = probability that different sexes avoid traps at equal frequencies (N.S. = $p > 0.05$)

2. Antennal damage

Analysis of data collected between May and July 1987 showed that the proportion of individuals of the population exhibiting antennal damage fluctuates temporally. Since the ratio of the number of beetles examined from pitfalls to the number examined from quadrats was not kept constant, the data have been subdivided according to date. Three periods were chosen in 1987: 6th May to 20th May (Period 1), 3rd June to 17th June (2) and 20th June to 30th June (3).

No significant difference was found, during each of these periods, between the frequency of beetles with damaged antennae in pitfall traps and the frequency in quadrat samples (Table A6.3). This suggests that damaged antennae

do not increase the chance of beetles being captured. It is clear that a higher proportion of individuals of *B. lampros* than of *B. quadrimaculatum* have damaged antennae but no explanation for this difference was found.

The results of the second method, which incorporated the rate of encounter of the two groups, are presented in Table A6.4. These support the findings of the indirect method using field data. No significant difference exists between the avoidance rate of beetles with damaged antennae and beetles with the full complement of antennal segments. However, once again the data are sparse since the frequency of beetles with damaged antennae in the population is low.

Table A6.3

		P i t f a l l s			Q u a d r a t s				
Period	Species	A Ncap	B Observed freq. damaged	C Expected freq. damaged	D Ncap	E Observed freq. damaged	F Expected freq. damaged	Chi Square	p
1	B. quad.	30	3	1.85	35	1	2.15	1.33	NS
	B. lanpros	41	8	5.54	33	2	4.46	2.45	NS
2	B. quad.	22	3	1.53	50	2	3.47	2.03	NS
	B. lanpros	68	13	11.92	29	4	5.08	0.33	NS
3	B. quad.	58	6	7.47	43	7	5.53	0.68	NS
	B. lanpros	96	20	20.87	19	5	4.13	0.22	NS

$$C = (B+E) \times A / (A+D)$$

$$F = (B+E) \times D / (A+D)$$

p = probability that beetles with damaged antennae occur in pitfalls and quadrats at equal frequency (NS = $p > 0.05$)

Table A6.4

Species	T r a p p e d			A v o i d e d			Chi Square / p	
	A Observed Frequency encounter	B Observed Frequency damaged	C Expected Frequency damaged	D Observed Frequency encounter	E Observed Frequency damaged	F Expected Frequency damaged		
B. lanpros	17	3	2.47	45	6	6.53	0.157	N.S.
B. quad.	24	1	1.09	42	2	1.91	0.012	N.S.

$$C = (B+E) \times A / (A+D)$$

$$F = (B+E) \times D / (A+D)$$

p = probability that beetles with damaged antennae avoid and are trapped by pitfall traps at equal frequencies

3. Antenna length: body length ratio

Mean data of body length, antennal length and the ratio of the latter to the former are presented in Table A6.5. The ratio lies between 0.4 and 0.5 for most species, *Notiophilus biguttatus* being the most noticeable exception at 0.307. If the arc sine of the proportion of individuals of each species avoiding (Table 4.3, Chapter 4) is regressed upon this mean ratio then no significant relationship between the two variables is found ($r=0.0243$, d.f.=6, $p>0.05$).

Table A6.5

Species	Mean Antennal Length (mm) (A)	Mean Body Length (mm) (B)	Mean A:B ratio	No. of Individuals Examined
<i>N. biguttatus</i>	1,491 $\pm$ 0,026	4,872 $\pm$ 0,109	0,307 $\pm$ 0,009	10
<i>P. melanarius</i>	5,788 $\pm$ 0,068	14,322 $\pm$ 0,243	0,405 $\pm$ 0,009	10
<i>B. quadrimac.</i>	1,451 $\pm$ 0,018	3,193 $\pm$ 0,044	0,455 $\pm$ 0,010	10
<i>B. lampros</i>	1,711 $\pm$ 0,030	3,580 $\pm$ 0,057	0,479 $\pm$ 0,011	11
<i>B. lunulatum</i>	1,778 $\pm$ 0,042	3,798 $\pm$ 0,065	0,468 $\pm$ 0,008	10
<i>B. guttula</i>	1,457 $\pm$ 0,020	3,066 $\pm$ 0,052	0,476 $\pm$ 0,006	10
<i>A. muelleri</i>	3,374 $\pm$ 0,095	6,940 $\pm$ 0,105	0,486 $\pm$ 0,013	5
<i>B. tetracolum</i>	2,622 $\pm$ 0,043	5,164 $\pm$ 0,052	0,508 $\pm$ 0,009	10

Discussion

The three investigations outlined above attempt to relate differences in sex or external structure to avoidance rate of pitfall traps. Both direct and indirect methods suggest that

- a) The sex of conspecific carabids does not affect the rate of avoidance of pitfall traps
- b) Beetles with damaged antennae are captured by pitfall traps at a frequency which does not differ significantly from the frequency at which conspecifics with normal antennae are captured
- c) The relative length of antennae can not be directly related to the rate of avoidance exhibited by a species.

The investigations regarding the sex of beetles and damaged antennae were limited in some ways. Firstly, the field data did not take into account the rate of encounter of the two groups being compared - it may be that females and males of a particular species are differentially active, or beetles with damaged and undamaged antennae are differentially active and thus the probability of encountering a pitfall trap would not be equivalent for individuals of each group. The data which did take into account the rate of encounter was sparse, with low values being recorded particularly for the observed frequencies at which beetles with damaged antennae encountered traps. This could not be overcome by simply increasing the number of beetles with damaged antennae which encountered traps in the laboratory since this feature can only be seen easily in dead specimens. However, it is conceded that CO₂ gas could have been used to anaesthetize beetles to facilitate examination.

It is not known whether the antennae of beetles collected from quadrats

can be damaged by passage through the pooter. It would be necessary to test this independently by subjecting a control group of beetles to a less forceful method of collection and then comparing the frequency of damage in the two groups. This is necessary because if the possession of damaged antennae does increase the probability of a beetle being captured by a pitfall trap, this might not show up in a statistical analysis of field data if beetles' are being damaged by the technique which is used to collect individuals and on which the expected frequency of damage is based (i.e. the control group).

The techniques outlined above warrant further investigation before any firm conclusions are drawn about intraspecific or interspecific differences in avoidance rates. It should also be stressed that there are likely to be other possible causes of differing rates of avoidance. It can be tentatively concluded from the results presented above and in Chapter 4 that body length is so far the only feature which has been shown to be related to the rate of avoidance of a species.

Appendix 7

Statistical Equations

1. REGRESSION

Residual Mean Square

$$s_r^2 = [\sum (Y - \bar{Y})^2 - (B^2 \times \sum (X - \bar{X})^2)] / (N-2)$$

where B = regression coefficient

$\bar{Y}$ = mean of Y

$\bar{X}$ = mean of X

N = number of pairs of variables

Standard Error of Regression Coefficient

$$SE_B = [s_r^2 / \sum (X - \bar{X})^2]^{1/2}$$

Standard Error of y

$$SE_y \text{ at } X' = s_r * \{N^{-1} + [(X' - \bar{X})^2 / \sum (X - \bar{X})^2]\}^{1/2}$$

2. t - TESTS

Difference between the means of two small samples ($N_1 + N_2 < 30$)

$$s_c^2 = [\sum x_1^2 + \sum x_2^2] / [N_1 + N_2 - 2]$$

where s_c^2 = combined estimate of variance.

x = $(X - \bar{X})$

N = number of cases

subscripted numbers refer to respective samples

$$t = \bar{X}_1 - \bar{X}_2 / [s_c (1/N_1 + 1/N_2)^{1/2}]$$

where t has $[N_1 + N_2 - 2]$ degrees of freedom

Difference between the means of two large samples ($N_1 + N_2 > 30$)

$$t = (\bar{X}_1 - \bar{X}_2) / [(s_1^2 / N_1) + (s_2^2 / N_2)]^{1/2}$$

where $\bar{X}$ = mean, s = standard deviation, N = number of cases

Subscripted numbers refer to the respective samples.

t has $(N_1 + N_2 - 2)$ degrees of freedom.

3. Mann-Whitney U test

$$U = N_1 \times N_2 + N_1 (N_2 + 1) / 2 - \sum R_1$$

$$z_U = U - [N_1 \times N_2 / 2] / \{ [N_1 \times N_2 (N_1 + N_2 + 1) / 12]^{1/2} \}$$

where U = Mann-Whitney U statistic.

N_1 = Number of values in first sample.

N_2 = number of values in second sample.

R_1 = Rank of values in first sample when values of both samples are ranked in order of increasing size.

z_U = z score for comparison with tabulated values of z for probability distribution.

Appendix 8

A recent relevant publication

The work of Halsall & Wratten (1988) was published just prior to the submission of this thesis. It considers pitfall-trap efficiency with respect to 7 species of polyphagous predatory Carabidae: *Demetrias atricapillus* (L.), *Notiophilus biguttatus*, *Trechus quadristriatus* (Schrank), *Agonum dorsale* (Pont.), *Calathus melanocephalus* (Goeze), *C. fuscipes* (Goeze) and *Nebria brevicollis* (F.). Only *N. biguttatus* was common to both studies and the experimental conditions differed but the results are still worthy of discussion.

Pitfall trap efficiency is defined, as in the present study, as the proportion of encounters resulting in capture. The term avoidance is also used. I have preferred to use the rate of avoidance as opposed to the rate of capture, for reasons outlined in Chapter 1, but the sum of the two parameters is 1 for any one species and should not lead to confusion.

Efficiency was determined in the laboratory using time-lapse video recording of beetles in an arena with a surface area of 0.25m² which contained four pitfall traps (diameter at perimeter = 8cm). The traps did not contain any preservative fluid. All species were released into the arena for a continuous 24 h period. The maximum experimental density was 425 beetles m⁻² and multiple encounters were possible.

Capture rates were found to be consistent even when the substrate was changed (from silver sand to soil) or when beetles were collected from the field at different times of the year. The capture rates were found to be low for all species (i.e. high avoidance rates). Avoidance rates given in Figure 1 (experiment 1: silver sand) (p.296) are quoted in Table A8.1 of this appendix where they are statistically compared with the estimated rate

of avoidance (determined using the regression equation in Fig. 4.2 of this thesis [except for *N. biguttatus* whose actual rate of avoidance is used]). *D. atricapillus* is excluded from this analysis because it was found, in the present study, to be capable of 100% avoidance and considered unrepresentative of carabids. The tarsi of this species are well adapted to adhering to a variety of smooth structures such as plant stems and this enables the beetles to avoid capture by maintaining contact with the inner wall of a plastic cup even after contact with the trap perimeter has ceased (own observations). Indeed the authors found that the highest capture rate for this species was only 0.01.

Table A8.1

Analysis of data presented by Halsall & Wratten (1988)¹

Species	no. of encounters	frequency of avoidance	predicted ² frequency of avoidance	Chi square	p
<i>N. brevicollis</i>	45	34	15.84	20.81	***
<i>N. biguttatus</i>	60	51	52.00	0.02	N.S.
<i>T. quadristriatus</i>	38	34	28.60	1.06	N.S.
<i>A. dorsale</i>	47	44	28.20	8.85	**
<i>C. melanocephalus</i>	50	44	29.00	7.76	**
<i>C. fuscipes</i>	42	30	14.28	17.30	***

1 Data from their Fig. 1, experiment 1 (p.296).

2 Predicted from mean body length (Lindroth, 1974 or own data) and the regression equation presented in Fig. 4.2 of this thesis except for *N. biguttatus*, the avoidance rate of which was determined in the present study (Table 4.3).

p=probability that null hypothesis is upheld (***=p<0.001; **=0.001<p<0.01; N.S.=p>0.05).

As can be seen from Table A8.1, significant differences exist between the observed frequency of avoidance according to Halsall & Wratten, and the expected frequency of avoidance according to the linear equation relating beetle body length to avoidance rate for four of the 6 species for which data was analysed. This is to be expected since the authors found no relationship between capture rate and beetle size (body length). Possible explanations for the observed differences may be found in the different experimental conditions used. These are summarized in Table A8.2 for both studies.

Table A8.2

Experimental conditions for the determination of rates of avoidance

	Halsall & Wratten	This study
Temperature	15 (± 2)°C	18 (± 1.5)°C
Light (night)	3 μ E/m ² /s	5 μ mol/m ² /s
Food	2nd-4th instar larvae of <i>Acyrtosiphon pisum</i> (Harris)	Fish pellets and crab paste.
Periodicity	16 h light; 8 h dark	14-16 h light; 8-10 h dark
Substrate	silver sand	Plaster of Paris
Preservative	none	50% (pbv) ethane diol
Diameter of trap at perimeter	8.0cm	5.5cm
Trap material	polystyrene	rigid PVC
Multiple encounters	Yes	No
Observation	indirect (video)	direct (human)

It was argued in Chapter 7 that avoidance rates should only be compared if identical traps are used. This argument is also put forward by Adis (1979) in his review of pitfall methodology. Luff (1975) and Waage (1985) have also shown that traps of different structure capture carabids at different rates. Nevertheless, since such little work has been done on pitfall-trap efficiency, comparison of results can still be beneficial despite differences in materials and conditions.

Dry traps were used by Halsall & Wratten whereas 50% ethane diol was used in my own studies. The effect of this solution on behaviour prior to and during encounters is still not clear since this was only tested for two species (*N. biguttatus* and *B. quadrimaculatum*). The other important difference between the two studies, and one that might explain the different rates of avoidance observed, is the fact that multiple encounters took place in Halsall & Wratten's study but not in the present study. If beetles are able to learn to avoid traps then avoidance rates will be artificially high where multiple encounters occur. This would particularly affect data for larger species since individuals of these species are likely to encounter traps more frequently than individuals of smaller species (see Chapter 6 of this thesis). The greatest differences between the two sets of results are for the two relatively large species *N. brevicollis* and *C. fuscipes*. As large species these would, according to the present study, have relatively low rates of avoidance. The authors found this not to be the case and the difference is difficult to explain in the absence of any evidence that multiple encounters can affect avoidance rates.

Rather than attribute the interspecific differences within their own set of results to beetle size, Halsall & Wratten suggest, in their discussion, that capture rate (or avoidance rate) is most likely to be related to relative visual acuity. The significance of the regression

equation presented in this thesis was dependent upon the inclusion of the two large nocturnal *Pterosticus* species. It may be the fact that they are both nocturnal, rather than simply large relative to other species, that results in them having a relatively low rate of avoidance. If this were the case then all nocturnal species might be expected to have low avoidance rates but *C. fuscipes*, which was active during periods of light and darkness in the study under discussion, was found to have a lower avoidance rate than the exclusively nocturnal *C. melanocephalus*. This might suggest that it is a combination of both factors - size and perception - which determines avoidance rates.

It may be that a simple interspecific relationship is not possible when many different species are considered, and that the avoidance rate of each species must be determined experimentally and not predicted. In order to determine whether this is the case, a large number of species should be studied under identical conditions.

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Estimation of population densities of carabid beetles in cereal crops

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ABSTRACT

A model is presented which aims to predict population densities of carabid beetles from pitfall-trap data. This is not normally possible because of interspecific differences in activity patterns, resulting in differences in the rate at which individuals of different species encounter traps. Experiments carried out both in the laboratory and in the field on 10 species of Carabidae reveal that another factor, the rate of avoidance of traps following encounters, also differs interspecifically and should be taken into account before any predictions of abundance using pitfall-trap data are attempted.

Data on the activity patterns of 5 of these species is used to simulate movement of individual beetles on a hypothetical grid of pitfall traps in the memory of a computer. Activity is simulated for a number of different durations and the proportion of individuals of each species encountering traps is determined for each duration. This parameter is regarded, for each species at each duration, as an estimate of the probability of an individual encountering a trap in the field.

This parameter is combined with the avoidance rate to modify pitfall-trap data collected over an equivalent period. This gives a modified estimate (corrected for activity and avoidance) of the relative abundance of species in pitfall traps. This relative abundance is compared interspecifically with absolute abundance estimates from the field to determine the accuracy of the model.

A discussion of the assumptions accompanying the model is followed by suggestions for further refinements so that it might be used in the future to predict the absolute abundance of carabids which are natural enemies of agricultural pests such as aphids.