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Abstract

The study consisted primarily of a number of surveys in brassica
fields, using pitfall and gutter traps. At all sites a number of
different species of carabids were marked and released. From the
pitfall trapping it was found that different carabid species
inhabitated different parts of the field, particularly in relation to
the field boundaries. Two common species, Nebria brevicollis and
Bembidion lampros, over-wintered in the hedgebanks, moving out into
the fields in the spring. Two other common species, Pterostichus
melanarius and Harpalus rufipes, were primarily associated with the
field, but activity in the field boundaries continued later into the
year.
    Marking concentrated on four species; P. cupreus, P. melanarius,
H. rufipes and N. brevicollis. At all sites the recapture rate of H.
rufipes was much lower than that of P. melanarius, though they are of
similar size. Using this data, mean displacement/day was calculated
for each species.
    To identify the causes for the differences in recapture rate
between the species, two species were individually tracked at night,
in the field. Positions every two minutes were recorded and the
distance and turn between each point measured. The results showed
that H. rufipes had a higher turn rate and moved less than P.
melanarius.
    The data from tracking was incorporated into a computer simulation
model which recreated the beetles' tracks, using the same time
interval. Traps were added and the model used to simulate the
recapture experiments in the field. Changes in dispersal patterns
were used to create differences in the catch in different patches. It
was found that changes in turning behaviour could not produce changes
in density, because of behaviour at the boundaries. Delaying the
change in behaviour produces differences in numbers, but orientation
is the most likely mechanism. The relationship between step length,
turn and catch was also evaluated.

Contents

1.1 INTRODUCTION TO THE CARABIDAE

The Coleoptera, or beetles, form the largest order in the class Insecta with some 280,000 species recorded so far (Daly et al 1978). In terms of abundance they are a highly successful group, exploiting a wide range of habitats and utilising some niches almost to the exclusion of other insect groups. The majority are terrestrial herbivores, though some families are entirely or partially predaceous and others are highly successful in aquatic habitats.

Beetles are characterized by the modification of the fore-wings to form hard protective cases, the elytra, to protect the membranous hind-wings. The mouthparts are adapted for chewing with recognisable mandibles, maxillae and labium. They are endopterygotes and the larvae are very variable ranging from free-living predators to wood-boring larvae which have lost or reduced legs and sensory organs.

The order is divided into four sub-orders, two of which are very small and the main one is the Polyphaga with about 90% of the known species. Carabids belong to the remaining sub-order, the Adephaga, of which they are the largest family. Other families in the sub-order include the aquatic families of beetles such as Dytiscidae, Gyrinidae and Hapliplidae.

The Adephaga are distinguished by the possession of metacoxae which are effectively fused to the first abdominal segment. The antennae are long filiform or moniliform and they retain 5 tarsi on each leg. Despite being a very large family the carabids demonstrate a high degree of morphological uniformity. There are approximately 40,000 species (Thiele 1977), the majority of which are ground-living predators, hence the popular name - Ground Beetles. In size they range from 1-50mm. The legs are usually long and they are effective
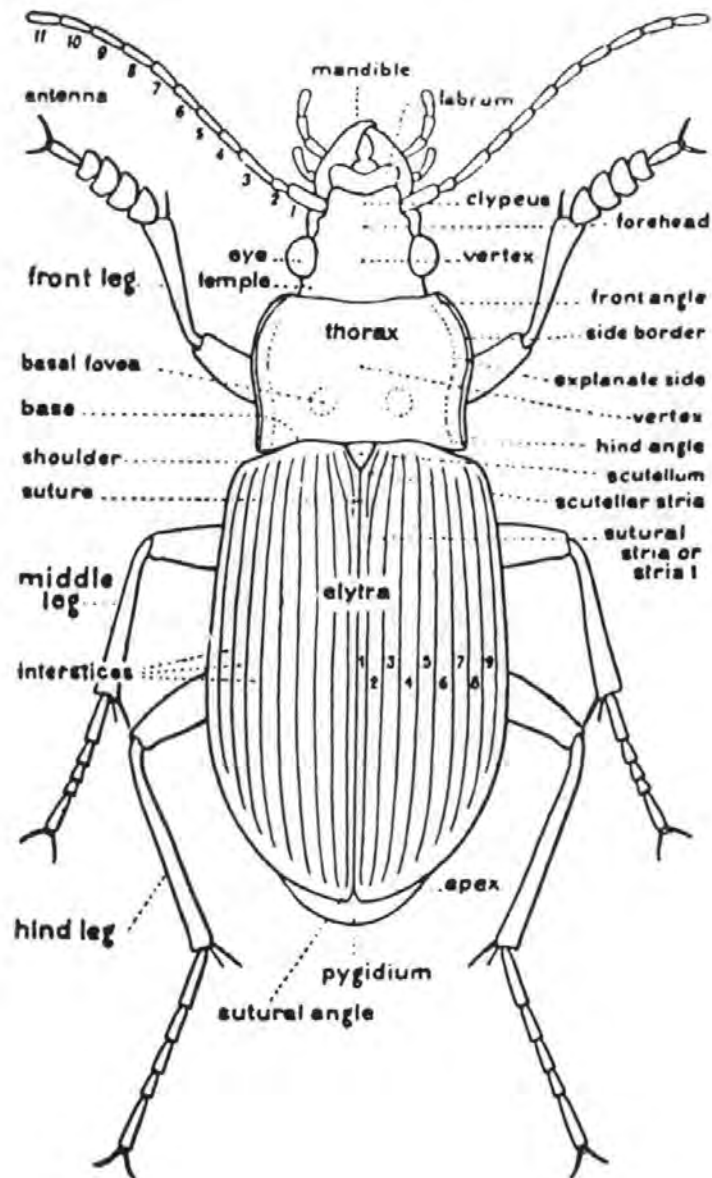
Figure 1.2:
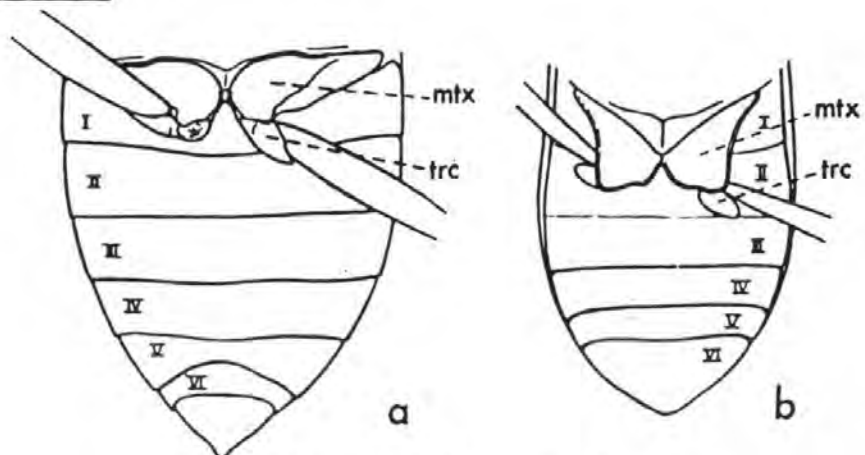
.—Underside of abdomen in (a) a Silphid; (b) a Carabid beetle.
mtx, meta-coxa; trc, trochanter. I—VI, visible sternites.

(From Lindroth 1974)

runners, though in some genera the front legs are specialised for digging. There are six visible sternites (fig.\.2), except in Brachinus. The vast majority of the larvae are campodeiform with two claws on each leg and are mostly subterranean predators.

As polyphagous predators the majority eat a wide variety of invertebrate prey. These range in size from large caterpillars and earthworms to mites and invertebrate eggs. Carrion and damaged or injured prey form an important part of their diet and these may be chosen in preference to intact prey (Mitchell 1963a). The prey does not have to move in order to be taken, static prey being acceptable. Most of the species eat a wide range of prey items though some are highly specialised. As examplesCalosoma inquisitor (L.) is a specialist caterpillar predator and Cychrus caraboides (L.) feeds on mollusca.

Some groups, particularly in the genera Harpalus and Amara, are primarily or entirely seed feeders. However many predominantly predatory species may include vegetable matter in their diet particularly at certain times of the year (Thiele 1977). Prey recognition is probably mostly by physical contact and chemical stimulation. However some carabids are visual predators such asNotiophilus biguttatus (Fab.) which is a specialist predator of collembola and orientates towards moving prey (Ernsting 1977).

The majority of carabid species are not ready fliers, many have lost their hind-wings or are dimorphic. In flightless individuals the hind-wings are usually much reduced, though in some species with normal wings the musculature may be atrophied paralleling the situation found in the Staphylinids. Paarman (1966) found that in the flightlessPterostichus oblongopunctatus (Fab.) the ratio of body length to wing length was 1:0.68, much lower than in a related species

which does fly, P. angustatus (Dufts.), where the ratio was 1:0.94.

Flight may be restricted to a short period of the life cycle, for

example Carter (1976) in Canada showed that in Agonum retractum

(Leconte) the females are only capable of flight for a short period

between coition and until the eggs develop, after which the wing

musculature atrophies.

In contrast to flight the majority of species are excellent

runners and may disperse over long distances on the ground. Den Boer

(1971) suggests that there is long-range 'migratory' walking in

carabids in Holland. From detailed structural studies Evans (1977)

suggests that the group can be divided into three different

specialisations; 'runners', 'wedge-pushers' and 'burrowers' each with

their own characteristics. The restricted movement of the hind coxae

in carabids allows the rotation of the hind femur on the trochanter.

This means that the hind legs can exert an upward as well as a forward

force and Evans considers this to be important in wedge-pushing. The

original habitat of beetles may have been pushing underneath bark

(Crowson 1981) and the wedge-pushers possess stout legs and large hind

trochanters allowing them to push under stones or soil in search of

prey and to utilise crevices in the ground as refuges (Evans 1977).

The runners are modified wedge-pushers which have developed long thin

legs, small hind trochanters and have sacrificed the ability to force

underneath objects in order to run rapidly. The final group, the

burrowers, have large front tibiae and often a narrow 'waist', as

their name suggests they are adapted for a subterranean life.

The runners include genera such as Cindela, Leistus and Nebria,

whilst the wedge-pushers include many Pterostichus and Abax and the

burrowers include Clivina and Dyschirius. Evans (1977) measured the

speed of movement of a number of species and found that the first

group all exceed 20 cm/s, with the highest figure for <u>Cicindela</u>

<u>hybrida</u> (L.) of 58 cm/s. Large wedge-pushers all had maximum speeds

below 20 cm/s and Clivina less than 1.5 cm/s.

The breeding cycle of carabids can be classified into a number of

different groups (Thiele 1977). These are listed below:-

1. Spring breeders with summer larvae, overwintering as

   adults.

2. Species which have winter larvae and reproduce from

   summer to autumn with adult dormancy.

3. Species which overwinter as larvae but the adults aestivate

   between the spring emergence and autumn breeding.

4. Those with flexible reproductive periods, i.e.

   they can breed in spring or autumn with the larvae developing

   equally in both periods.

5. Species requiring more than one year to develop.

The spring breeders are normally active during May and June after

which activity drops off, examples include <u>Pterostichus cupreus</u> (L.)

and <u>Bembidion lampros</u> (Herbst). There is often another peak of

activity in the autumn, before overwintering, of adults which have

emerged that year. Carabids in the second group have their main

period of activity in mid-summer becoming inactive in the autumn,

though in the spring there may be some activity of adults which have

over-wintered. Species from the next group have a peak of activity in

the spring from both over-wintering and emerging beetles, but these

are dormant during July and August and are found in large numbers from

September. Examples from these two types include <u>P. melanarius</u>

(Illiger) and <u>N. brevicollis</u> (Fab.) respectively.

Carabids are unusually long-lived insects (Crowson 1981) and a

substantial proportion of the adults may live for more than one

breeding season. In Holland Vlijm (1968) found that 60% of Calathus
melanocephalus (L.), an autumn breeder, overwintered. Van Dijk (1979)
found that the same species usually lived for two years, with
mortality occurring in the winter, and a larger species, Pterostichus
coerulescens generally lived for three to four years, mortality being
highest in the breeding season. Murdoch (1966) suggests that there
was an inverse relationship between the amount of breeding in one
season and survival to the next and that this compensatory mechanism
led to stability in carabid populations. Van Dijk (1979) found no
evidence in the two species he studied to support this hypothesis but
suggested that old beetles are of high importance to the population
survival because of the heterogeneity increasing the stability under
varying environmental conditions.

The over-wintering site of the adult beetles varies according to
the species. Many of the larger species, such as P. melanarius and
H. rufipes (Degeer) overwinter in the field itself often deep in the
soil (Scherney 1961). Other species may migrate to the field
boundaries or into woodland and may be found overwintering at the base
of tree stumps (Thiele 1977). Southerton (1985) sampled a variety of
types of field boundary and found that Bembidion lampros was found
mainly in hedge-banks whilst Agonum dorsale (Pont.) over-wintered
mainly in the grassy edges.

In spring the overwintering carabids migrate out into the
adjoining field as was shown for A. dorsale (Pollard 1968, Coombes &
Southerton 1986) and in Bembidion lampros (Wallin 1985). The last
author also found evidence for a migration in the autumn back to the
field edges.

The majority of carabids are nocturnal but some are diurnal or
active both day and night. Luff (1978) and Desender et al (1984) have

used time-sorting pitfall traps and show the daily activity rhythm for a number of different species. The majority peak around midnight however there is a great deal of variation. As a general rule Luff found that larger species tended to be nocturnal as did autumn breeders, whilst spring breeders were mainly diurnal. In H. rufipes (Luff 1978) and P. melanarius (Desender et al 1984) the main peak of activity showed a temporal shift through the season. Individuals also show flexibility and nocturnal species may become active during the day in certain habitats or if they become hungry.

Much less is known about the larvae of carabids. The majority feed on a variety of small invertebrates although as with the adults, they may be specialist predators or seed feeders. They are soil dwelling and some, particularly N. brevicollis, may be highly surface active at certain times, being caught in large numbers in pitfall traps (Greenslade 1964b).

As with any animal, individual species of carabid are associated with certain kinds of habitat. Agricultural fields form an unnatural and often unstable habitat and the carabid communities associated with them appear to be fairly uniform across Europe. Thiele (1977) lists eight different species which are particularly frequent and characteristic of cultivated land. These occurred in two-thirds of a list of 29 arable sites stretching from England to Byelo-Russia. The species are as follows; P.melanarius, P. cupreus, H. rufipes, H. aeneus (Fab.), Agonum dorsale, A. muelleri (Herbst), B. lampros and Trechus quadriatus (Schrank).

To these may be added N. brevicollis which is particularly frequent in cultivated sites in Western Europe.

1.2 Carabids in Research

Carabids have attracted the attention of researchers for a number of different reasons. Primarily this has been due to their abundance and position as one of the main elements in any fauna. More recently their potential as agents of pest control has meant that a number of aspects of their biology have been extensively studied. Much of this work is covered in an excellent review by Thiele (1977) but an overview of the research is presented here.

The biology and ecology of individual species has been the subject of much work, particularly on species which are likely to be effective predators of pests such as aphids. Mitchell (1963a, 1963b) studied B. lampros and T. quadristriatus using a variety of techniques including pitfall trapping and quadrats and also gut dissection to identify prey. N. brevicollis (Greenslade 1964b, Penney 1966) and P. madidus (Fab.)(Luff 1974) are other examples of intensively studied species whilst there are also a number of general studies. Most of this research has been in agricultural situations, particularly cereals (Jones 1976,1979,Ericson 1979) but also in brassicas (Mitchell 1963a, Dempster 1968b, Anderson 1982)

Work on the general biology of carabids has shown that they are useful predators and are often present in agricultural habitats at suitable times to exert an influence on prey populations. However there is doubt as to whether the beetles consume pest species in particular or whether they feed mainly on non-pest invertebrates. Thus there have been numerous studies on the effect of carabids on pest populations and also on the diet of various carabid species. These are often of the form where different areas are treated so as to reduce or increase carabid density by using barriers and insecticide.

Wright et al (1960) carried out similar experiments and showed that carabids, together with staphylinids, were responsible for the loss of 90% of Cabbage Root Fly (Delia radicum, Pont) eggs laid. This highlighted the importance of B. lampros, also shown by Andersen et al (1983) to be the most effective predator of the Turnip Fly (D. floralis). Carabids are also important predators of aphids (Sunderland & Vickerman 1980, Griffiths 1982), mostly when the aphids fall to the ground, though some carabids are proficient climbers.

The work mentioned above has shown that ground beetles do exert an influence on pest populations but normally not sufficient to avoid the necessity of applying pesticides. The effect of these insecticides on the beetles themselves and the efficiency of the insecticides and carabids together has been explored by Coaker (1966) and Dempster (1968a, 1968b) in brassicas and in cereals by Edwards & Thompson (1975) and Chiverton (1984). These studies show that apart from causing mortality there are also sub-lethal effects, particularly on small species, which cause an increase in activity (and hence numbers caught in pitfall traps). Mowat & Martin (1981) could not find a significant effect of insecticide and carabids together in cauliflowers, but that by themselves the predators were responsible for 40% of the loss of Cabbage Root Fly. It has been shown that ground beetles are more abundant on organic than on conventional farms (Dritshilo & Wanner 1980, Dritschilo & Erwin 1982).

In order for the polyphagous predators in agricultural habitats to be effective it is necessary to encourage them as much as possible. A number of carabid species use field boundaries as overwintering sites and migrate into the field each year. Pollard (1968a) showed the importance of hedgerows, particularly as a site for A. dorsale, and the detrimental effect of removing hedge flora on the polyphagous

predator populations. Other field boundaries such as shelterbelts
(Lyngby & Nielson 1980) and grassy edges (Desender et al 1981,
Desender 1982) are also utilised by carabids whilst Sotherton
(1984,1985) has shown that different species require different types
of overwintering sites and so the various field boundaries (and the
field itself) contain different species of beetle.

Within the field the effect of crop cover and weed density has
been investigated (Dempster 1969, Speight & Lawton 1976, Ryan et al
1980, Powell et. al. 1985). They have shown that variations in the
crop have an effect on the micro-climate and that increases in the
weed cover can increase the numbers of carabids caught, however the
relationship is inconsistent.

In order to assess the importance of carabids as predators of
pests it is neccessary to estimate the density of beetles in
agricultural situations. A number of studies have used mark/recapture
techniques using individually marked beetles and pitfall trapping.
Ericson (1977) estimated densities of 0.64 inds/m^2 for P. cupreus and
0.73 inds/m^2 for P. melanarius in winter wheat using Jolly's
Stochastic Method. Best et al (1981) found slightly lower values for
three similar American species in maize. They considered that the
populations, which all had aggregated dispersions, were stable in time
with little dispersal occuring. Population estimates for
over-wintering beetles have been made using soil core techniques
(Sotherton 1984, 1985, Desender 1982) and Holliday & Hagley (1979)
found an unusually high density of carabids (289.1 m^2) in an apple
orchard using soil cores and sod samples (0.3mx0.3m sections removed
with a spade).

In addition to research on carabids associated with their
potential in pest control there is a large body of research on the

general ecology of the group, often in non-agricultural habitats such as forests, heaths or in specialised areas such as caves. Grum (1971,1975a,1975b) has carried out studies particularly on woodland carabids in order to elucidate their population ecology. He has shown that carabids change their activity and dispersal pattern in relation to satiation, increasing activity when hungry and becoming more directional in their dispersal. The population ecology of carabids is also the subject of long term research by Den Boer (1972,1977,1981,1982) particularly on how populations survive in a heterogeneous environment and the work suggests that if beetles are collected in pitfall traps for long periods (preferably over a whole year) then the numbers caught are a direct estimate of density and can be compared with other years and sites. This is, he hypothesises, due to a limited total amount of activity carabids need to complete during their life cycle. This was supported by Baars (1979) who subsequently used radio-active marking to track individual carabids (Baars 1980). The work suggested that the beetles alternated periods of small distances covered in random directions with periods of high mobility and directional movement, each period lasting a number of days. The directed walking was associated with unfavourable habitats and reflects Grum's research mentioned above. The same pattern of movement was found in Carabus problematicus (Rijnsdorp 1980) who showed that the species could orientate towards a forest silhouette (its preferred habitat) and could avoid moving into unsuitable patches.

The group has also been used as a vehicle to test specific aspects of ecological theory. Lenski (1982,1984) looked for competition between two forest species of Carabus and found evidence for the occurrence of both inter- and intra-specific competition.

There was no evidence, however, for lack of foraging success limiting population density. Sota (1985) also found evidence for competition between two species of Japanese carabid by directly observing individuals at night. The work showed that the influence of the competition was slight, probably because the seasonal segregation of the species reproductive activity.

The community ecology of carabids is also being studied in a variety of habitats including grassland (Luff, pers. comm. and Butterfield & Coulson, 1983), woodlands (Dennison & Hodkinson 1984, Szysko 1983). It is possible to identify associations of carabid species in different environments and these can be used to identify and separate different types of habitat. This can be particularly useful in nature conservation where the group can be used as indicator species (Refseth 1980) for the effects of pollution (Freitag 1978).

Finally, although not directly related to carabids, the use of pitfall traps has been analysed. The problems of using the traps were underlined by Greenslade (1964) who showed that the effects of vegetation surrounding the traps and the varying behaviour of different species meant that results need to be interpreted with caution. Luff (1975) tested a number of different types of trap to determine the effect of size, shape and material and his results will be discussed in a later chapter.

1.3 Carabids in Britain

In Britain Lindroth (1974) identifies 353 different species of carabid, including the Cicindelidae, or Tiger-beetles, ranging in size from 2-30mm. Of the 65 different genera the largest is Bembidion (58 spp.) and other large or important genera include Agonum (22 spp.), Harpalus (33 spp.), Nebria (6 spp.) and Pterostichus (22 spp.). Their taxonomic and ecological status has been extensively studied and the British fauna can be identified using standard texts (Lindroth 1974, Joy 1932). They are also the subject of an active mapping scheme (Luff 1982).

There follow some notes on the biology and ecology of four species which were particularly important in this project. They are all characteristic of agricultural land and Table (1.1) summarises their habitat requirements.

Nebria brevicollis (Fabricius) Adult size: 10-14mm

This is a piceous to dark brown carabid with rufous appendages. It inhabits a wide range of habitats including woodland and agricultural land (Greenslade 1964b, Dennison & Hodkinson 1983). Pollard (1968) demonstrated that there was a relationship between this species and the hedges surrounding fields and believed that this was due to climatic effects of the crop and hedge. Lyngby & Nielsen (1980) suggest that adults overwinter in shelterbelts and migrate into the fields during May.

The species is an autumn breeder and shows summer diapause. The adults emerge in May and June, disappearing in July and August before breeding and laying eggs up till mid-November (Greenslade 1964, Penney 1966, Jones 1979). Activity may continue at a low level throughout

the winter. It is nocturnal with activity peaking around midnight (Luff 1978). Penney (1966) found that the prey was mainly small flies, Collembola, mites, spiders and earthworms. The relative numbers varied at different times of the year and Collembola were considered to be the favoured prey item. The species has also been shown to be a predator of aphids (Sunderland & Vickerman (1979). Penney states that all prey items were less than 4mm in length, though it will feed on much larger items of carrion.

The species is dimorphic as regards wings but rarely flies (Thiele 1977) and falls into Evan's (1976) 'runners' category.

Pterostichus cupreus (Linnaeus) Adult size: 11-13.4mm

This is a brassy, metallic species with a localised distribution in this country (Lindroth 1974). It is generally associated with drier, warmer habitats (Thiele 1977), though Pietraszko & Clerq (1981) state that it is hygrophilic. Ericson (1978) found that it had a similar distribution to P. melanarius, avoiding open areas. It feeds mainly on a variety of small to medium sized invertebrates but vegetable matter probably forms an important part of the diet at certain times of the year. It was found by Skuhravy (1959) that in the spring 67% of individuals caught contained vegetable material declining to 20% in the summer.

The species is a spring breeder, active from May and June until the late summer (Ericson 1978, Wallin 1985) and there may be an increase in numbers in late summer due to the emergence of new adults. Wallin found some evidence for migration to and from hibernation sites in the field edge. The species is primarily diurnal but is also active at night.

Pterostichus melanarius (Illiger)(vulgaris- Linnaeus) Adult size: 12-18mm

A large black carabid common in a variety of open habitats. It is known to prefer areas of crop with good cover (Baker & Dunning 1979, Ericson 1978) and to avoid open spaces. It is a catholic feeder preying on a wide range of invertebrates from Cabbage Root Fly eggs to large caterpillars (Coaker & Williams 1963, Davies 1953). The species is also known as a predator of aphids, though it does not climb, Sunderland (1975) found that 16% of those caught contained cereal aphid remains and Dunning et al (1979) found that it would eat 7.8 Aphis fabae in 24 hours.

P. melanarius is an autumn breeder with no summer diapause. Activity commences in late April and May, peaks in July and August before declining in mid-October (Jones 1979, Ericson 1978, Andersen 1982). Beetles active early in the season are over-winterers and the females of these, together with early emergers, were found to breed twice in a season (Jones 1979). The species is nocturnal and Desender et al (1984) found that there was a large increase in daytime activity in late August. Pollard (1968) could find no apparent association with hedges surrounding the field whilst Lyngby & Nielsen (1980) found a variable distribution and suggest that adults overwinter in shelterbelts adjacent to the field and migrate out as shown in N. brevicollis.

The wings are normally rudimentary and Evans classifies it as a 'wedge-pusher'.

Harpalus rufipes (De Geer) Adult size: 10-16.7mm

The final carabid is a piceous to dark brown beetle with lighter appendages, differing from previous species in that the elytra

are covered with short, dense setae. It lives in a wide range of habitats and is extremely common. Although it is a predator of Cabbage Root Fly eggs (Coaker & Williams 1963), aphids (Sunderland 1975, Dunning et al 1975) and the major predator of small white butterfly larvae (Pieris rapae) (Dempster 1967), it is also a seed feeder and is an occasional pest of strawberries (Briggs 1957). The larvae are seed feeders with a preference for grasses and Chenopodium album, caching the seeds in burrows (Luff 1980). The adults are efficient climbers, climbing plants to feed on seeds or prey (Dempster 1967, Lovei & Szenkiralyi 1984).

The carabid is an autumn breeder with an activity cycle similar to P. melanarius. It is active from May until September (Jones 1978) though Luff (1980) found activity from April to mid-November, a period longer than that of P. melanarius at the same site. H. rufipes, however is a biennual species; females do not breed in the year of emergence but overwinter and breed in their second season (Luff 1980). On the Continent different patterns have been found and the species' life cycle is annual. Baker & Dunning (1975) found that in sugar beet fields the beetle was caught mainly in July and August with very few found before this. It is not clear whether this was due to a different annual cycle or changes in the field causing the beetle to move in at this time.

In Pollard's (1968) study there was an association with the hedgerow whilst Lyngby & Nielsen (1980) found that it was captured mainly in the border zone close to the shelterbelt (though only low numbers were found). In contrast Wallin (1985) found no distinct pattern with large catches occurring in the centre of the field.

As would be expected it is nocturnal and Luff (1978) showed that whilst early in the season activity centered around midnight, later in

the year it became markedly earlier.

The species is macropterous and is known to fly on warm nights (Briggs 1965). However Tietze (1963) found that the flight muscles degenerate with age and flight is presumably restricted to young adults.

Table (1.1) is derived from Thiele (1977) and summarises the habitat requirements of the four species, together with the running speeds, where available (Thiele 1977).

Table 1.1: Micro-climate preferences of the different species

	Temp.			Humidity			Light			Speed
	Cool	Tolerant	Warm	Humid	Tolerant	Dry	Dark	Tolerant	Light	cm/s
N. brevicollis			X		X		X			12.4
P. cupreus			X			X		X		10.6
P. melanarius		X		X			X			8.9
H. rufipes			X			X	X			–

1.4 Carabids In Brassica Crops

Most of the research carried out on carabids in agricultural fields has been in cereals, particularly in relation to aphid predation. Thiele (1977) states that there are no known cases of any carabid species being associated with a particular crop plant, however there are micro-climatic differences between crops caused by the different structures of the plants. These and other effects lead to variations in the carabid fauna, especially in the proportions of different species found. As a crop brassicas provide a large degree of cover with a relatively weed-free and unobstructed soil surface.

Research in brassicas has concentrated on Cabbage Root Fly, and the effect of polyphagous predators on mortality, (Wright et al 1960, Coaker & Williams 1963, Coaker 1965). The effect of insecticides on the fly and its predators has also been the subject of study (Coaker 1966, Finlayson et al 1980, Mowat & Martin 1981). Similar work on the Turnip Fly (Delia floralis) has been carried out (Andersen et al 1983, Andersen & Sharman 1983) and Dempster (1967, 1968a, 1968b) investigated the predators of the small cabbage white butterfly and the effect of DDT.

These studies have shown that polyphagous predators and carabids in particular can exert a large influence in pest populations. B. lampros is considered to be the most important predator of both the dipteran pests whilst Dempster found that H. rufipes was the most important predator of the caterpillars. Dempster (1967) records finding this species actively climbing on the brussel sprouts in the study, together with T. quadristriatus, whilst B. lampros is mainly responsible for mortality of eggs on the ground.

Most of the papers do not give a total list of carabid species

found or were carried out in small plots surrounded by barriers. One study (Andersen 1982) does provide a comprehensive list of carabids found at a variety of brassica sites in Norway.

In general the most common species found through all the studies are those found in all agricultural situations; P. melanarius, B. lampros, T. quadristriatus, and H. rufipes. In Andersen's (1982) study Calathus melanocephalus and B. quadrimaculatum (L.) were also very common in the pitfalls. Other species which appear in numbers include C. fuscipes (Goeze), H. aeneus, Agonum dorsale and A. muelleri. N. brevicollis is not recorded in large numbers in many of the studies, but this is probably because it is only active early and late in the season, outside the period of trapping.

The effect of soil is probably as important as the crop itself, with large differences between sandy and clay soils. Andersen (1982) found P. melanarius was caught in much greater numbers at heavy soil sites rather than at a site with sandy soil and this was also found by Baker & Dunning (1979) in sugar beet. In general carabids are found in greater quantity on clay than on other types (Thiele 1977, Baker & Dunning (1979), Pietrasko & De Clerq 1980). The last mentioned authors also found much greater numbers of arthropods in general at clay sites, and so the numbers of carabid are likely to be responding to availability of prey.

The density of weeds in the crop also affects carabid density, probably because of their effect on micro-climate. In brassica this has been studied by Dempster (1969) and Ryan et al (1980). Both found that predation (on Pieris rapae larvae and Delia radicum eggs respectively) was greater in areas with the greatest weed cover (clover cover in Ryan et. al.). However Dempster found that only H. rufipes increased in numbers whilst Ryan et. al. found no clear

trend.

In contrast Speight & Lawton (1976) found that both numbers caught and predation increased in the areas with more weed cover, working in cereals. One complication which must be considered is that the weeds are likely to reduce carabid activity, particularly of the larger species, and hence the numbers caught (Greenslade 1964b).

1.5 Dispersal

Dispersal has been defined as any movement of individuals away from a population or aggregation (Southwood 1962, Dempster 1975), though there is much debate about this term and the use of the terms movement and migration. Thus dispersal here is used in the same sense as Stinner et. al. (1983) and refers to any movement by an individual, with movement referring to any action which results in a displacement of the animal. Baker (1978) used the term migration in a similar fashion and in an attempt to avoid the connotations of the other words, Hanski (1980) simply describes everything as movement.

Movements are often divided into two different categories e.g. the trivial range and migratory range of Southwood (1977). The first of these includes those movements of the animal during normal foraging or reproductive behaviour and they occur within the habitat of the animal. The second class includes movements between habitats and normally these involve a change in behaviour, with an increase in activity and directionality. Often the animal becomes insensitive to stimuli which normally cause it to cease moving (Johnson 1967) as is seen in the migration of aphids.

Powers of dispersal vary greatly between and within species. In carabids those individuals capable of flight can obviously disperse most effectively but long distances can also be covered on the ground. The larvae probably have only very limited capacity and are unlikely to move very great distances. Southwood emphasized the importance of dispersal in habitats which are temporary though Hamilton & May (1977) show that dispersal of a proportion of the offspring may be advantageous even in some stable environments. There are many reasons why animals should increase their rate of dispersal and Taylor & Taylor (1977)

suggest that it is primarily a response to density, and hence
dispersal is a density-dependant phenomenon. However from studies of
many carabid populations, Den Boer (1972,1977) has produced the
'founding hypothesis'. In this the function of dispersal over long
distances is primarily to maintain populations in a heterogeneous
environment and so it is greatest from the sparsest and least dense
populations, where the extinction of local populations is most likely.

The bulk of research on dispersal particularly that referred to
above, has been on movement by flight. The dispersal investigated
during this project has been on the ground and it is unlikely that the
individuals studied were capable of flying. However carabids are
capable of walking long distances: Baars (1979) found a P. versicolor
which had moved 87m in a day and Ericson (1977) measured a P. cupreus
covering over 50m/day. The average displacement for the population as
a whole is much lower than this with most individuals only covering a
few metres each day (Thiele 1977). Much of the data for daily
displacement is derived from marked beetles recaptured in grids of
pitfalls and is calculated for each of the recaptured individuals by
dividing the total displacement by the number of days since release.
Although this is not entirely accurate and is affected by the layout
of the grid, the values do give an indication of distances covered.
Ericson (1978) estimated values of about 3m/day for P. cupreus and a
similar value for female P. melanarius; male P. melanarius had a
slightly lower value during the period of study (2m/day). Somewhat
higher values have been found in some cases, Gordon & McKinlay (1985)
estimated 8.6m/day for P. melanarius and Best et. al. (1981) obtained
values of 10.5m/day, 12.2m/day and 10.2m/day for three species in an
American cornfield. Baars (1979) calculated values by following
individuals tagged with radio-active labels and used the results to

distinguish between two different types of movement; 'random walk' and ▸
'directed walk'. By measuring the distances and bearings between
daily positions for each individual Baars showed that during random
walk only small distances are covered each day in random directions.
Daily displacement for the two species studied was 2.5m/day
(P. versicolor) and 1.4m/day (C. melanocephalus) in this phase,
although it varied between habitats. In directed walk much greater
distances were covered with higher directionality, the values being
16.8m/day in P. vericolor and 9.3m/day in C. melanocephalus with the
average daily turn being 34° and 41° respectively. The directed walk
occurred particularly after the beetle had entered an unfavourable
habitat, which the carabids were unable to avoid entering. In a study
of a forest species Rijnsdorp (1980) also found evidence for two
different types of movement. The directed movement appeared in
individuals dispersing out of the forest, which moved more rapidly
than individuals recaptured inside the wood. The species studied,
P. problematicus, differed from those studied by Baars (1978) in that
they were able to avoid entering unfavourable habitats, according to
Rijnsdorp the species switched to directed movement at the edge of the
forest as a 'deliberate' choice in order to disperse from the area.
Those outside the forest were able to orientate towards the forest
silhouette and so return to their favoured habitat. The results from
Rijnsdorp's study differed from Baars' study where dispersal was
affected by factors such hunger or reproduction.

Grum (1971) and Brunsting (1983) have shown the effect of
starvation on carabids, with an increase in activity and
directionality. Grum found that populations of carabid could be
divided into two categories; satiated and unsatiated. In suitable
habitats the satiated beetles showed low mobility and the hungry ones

high mobility. In unsuitable habitats both groups showed high
mobility. This situation leads to a flow of beetles from suitable to
unsuitable habitats and back again. Mols (1978) has shown that
carabids, like many organisms, show area restricted search after
encountering a prey item, the amount of time spent in the search being
related to the level of hunger.

The foraging pattern of a predator is influenced by the
distribution of its prey. It is likely that prey will be distributed
in patches but these vary in size and stability. Jones (1977) showed
that caterpillars changed their search behaviour according to their
state if hunger and that the search pattern was related to the
distribution of the host plant. It was found that when Pieris rapae
larvae were removed from their food plant they moved slowly with a
high rate of turning. As they become hungry they become more
directional and increase their speed, behaviour appropriate as the
host plant occurs in small clumps. Another species, Plusia
californica, is polyphagous and so food plants are distributed more
uniformly does not show any change in behaviour as hunger increases,
but maintains directional search. Kane & Poulson (1977), studying two
species of carabid living in caves, have shown that the foraging
behaviour is related to the patchy distribution of prey and in
particular the carabids move between areas of suitable substrate in a
non-random fashion.

Using computer simulation models Hawkes (in Feeny 1982),
demonstrated that when distribution of habitats was independant of the
distribution in the previous generation, the most efficient foraging
pattern was straight movement for all patch distributions.
Alternatively, when the distribution of patches was dependant on those
in the previous generation a more conservative search

was advantageous, with a random walk being the most efficient under some circumstances.

1.6 Pitfall Trapping

A number of different methods are used to collect carabids, each with relative merits and drawbacks. The simplest of these is ground search, seeking beetles underneath stones or vegetation and this is useful in compiling a species list, but it is difficult to quantify estimates of density. To obtain more quantitative estimates of numbers three other main techniques have been used; pitfall traps, soil cores and D-vacs, with pitfalls being by far the most widespread method.

Soil cores have been used in a number of studies, usually to find over-wintering adults (Pollard 1968,Desender 1982, Southerton 1984, 1985) or in an attempt to measure absolute densities, possibly in conjunction with pitfall trapping (Desender et. al. 1983, Holliday & Hagley 1979). Normally fairly large quadrats of soil are dug out with a spade, usually to a depth of about 30 cm., or to bedrock. The method does provide valuable estimates of density but is impractical for many species as densities of carabid can be low ($<1/m^2$) and so large volumes of soil need to be sampled. Holliday & Hagley (1979) suggest that large active carabids such <u>P. melanarius</u> can avoid capture in soil cores and this is a further drawback. D-vac is mostly used to sample invertebrates on plants and on the soil surface, Vickerman & Sunderland (1975) used the technique in a survey of nocturnal activity in cereals.

Pitfalls themselves have the advantage that they can be used in large numbers to sample different areas of the habitat. They produce a great deal of data for long periods of time with relatively little effort involved. The problems associated with their use have been the subject of extensive discussion in the literature (Mitchell 1963b,

Greenslade 1964b, Kowalski 1976, Baars 1978). The main question is whether the results of pitfall surveys can be used to compare different sites and times and also to make quantitive comparisons between different species.

The total number of individuals caught is affected by a number of factors but in particular by the density of the beetles and by their activity (in terms of total distance covered on the ground during the trapping period). Mitchell (1963b) expressed the relationship in an equation;

$$C \propto f(A \times N)$$

where C is the catch per day, A is the activity, N is population density and f is a mathematical function. The activity is subject to a number of influences and these can be identified as follows;

1) Meteorological Factors— Temperature in particular affects carabid behaviour.

2) Vegetation— Greenslade (1964b) considers that dense plant growth will reduce the amount of movement.

3) Intrinsic Factors— There may be differences in behaviour between males and females as was found by Ericson (1977) and Grum (1971) showed that activity increases with hunger. These may also change through the life cycle of the species.

The actual number of individuals removed from the trap is also affected by a number of factors;

1) Ability of different species to avoid capture. Diurnal species may be able to see the trap and small or slow moving species be able to avoid falling in.

2) Escape from the trap. This may vary according to sex, species, flight ability and the material of the trap.

3) Position and Orientation of the trap. The placement of traps relative to plants is important and gutter traps are sensitive to any tendency for beetles to move in a particular direction.

Mitchell (1963a) found that T. quadristriatus remained in the shady areas underneath cabbages whilst B. lampros was mostly active on bare ground. This illustrates the last point, if traps are placed between rows of crops whilst carabids are concentrated around the plants then the pitfalls cannot give a clear picture of the fauna in the field. Similarly other objects such as barriers can have a dramatic effect on beetle distribution (pers. obs.).

Considering all these factors Greenslade (1964b) states that pitfalls cannot be used for "quantitative assessment of the carabid fauna of any habitat; nor should it be used to compare the numbers of one species in different habitats". Kowalski (1976) illustrates a situation where he considers that pitfalls do give an estimate of density which is comparable between different areas. Further Den Boer (1977) and Baars (1979) state that so long as pitfall trapping is carried out on a year long basis the results can be used to produce relative population estimates between sites and years. From this Baars concludes that carabids have an almost constant total amount of locomotory activity to 'use up' in a season. More recently Brunsting (1983) suggests that total annual locomotory activity does vary and so

the use of yearly captures as a measure of relative abundance is only possible when differences are large (at least 25%). Estimates are more accurate if temperature differences are allowed for.

A number of actions can be taken in order to reduce or quantify the variability inherent in pitfall trapping. Luff (1975) made a comparison of different types of trap and species of carabid. He quantified a number of features, including capture efficiency and retaining efficiency. From these studies it was shown that glass was the best material since it had a negligible escape rate. The mean capture efficiency (i.e. the number of beetles caught in proportion to those contacting the trap perimeter) was 70%, varying from 50% to 80% according to the species. Another finding was that small traps caught small species most effectively and vica versa, whilst traps could be compared on the basis of their total perimeter.

Hence in a survey consideration must be given to trap design. Large numbers ought to be used so as to reduce the effect of individual trap variation. Greenslade (1964b) recommends that the vegetation around each trap be removed so as to reduce differences between traps. It is best to sample for as long a period as possible, preferably for a whole year, although this may not be possible in an agricultural situation. Meteorological data, such as temperature, rainfall and wind, should be recorded on a daily basis.

The use of mark recapture techniques can add greatly to the information provided by pitfalls. The results can be used to estimate population density, dispersal rates and any directional movement of the carabids. Also proportion of marked to unmarked individuals in a sample, together with the total number caught, will give an indication as to whether changes in catch are due to variation in density or activity.

The numbers of beetles obtained by traps can be increased by using barriers to direct the catch, normally two pitfalls are placed at either end of the barrier (Reeves 1980, Wallin 1985). Alternatively baits can be used to attract carabids and the use of formalin may have the same effect (Luff 1968). Although this increases the yield it does add extra uncertainties because of the selective effect on different species. Because gutter traps are influenced by the direction of movement they can be used to observe the speed and timing of these movements, for instance migration away from over-wintering sites (Pausch et. al. 1979).

In the following section the design of the traps used in this study is described, together with other methods such as Mark and Recapture.

2.1 Materials and Methods: Trapping and Marking

As mentioned earlier, pitfall trapping is the most widespread method of sampling carabid populations and these were in use at all of the sites in the project. At some sites they were used in conjunction with gutter traps and soil cores. This chapter provides a description of the traps and the sampling techniques.

Pitfall Traps: Fig. (2.1a) shows the trap which was used throughout the study, the same one being used in order to reduce variation. These were made from glass and had the following dimensions; diam. 9cm, depth 11cm. They were produced from 1000ml amber, screw cap, wide-mouthed bottles with the tops cut off at the neck forming straight sided cylinders. Holes drilled in the bottom allowed drainage and inside were plastic inserts of the same diameter but only 4cm deep. To make the inserts flower pots were cut so that they fitted closely inside the trap. A single piece of nylon mesh covered the drainage holes in the pots and this was fixed in position with aquarium sealant.

Various kinds of mesh and methods of fixing them were tried but Simonyl N800 nylon gauze proved to be the most effective. The mesh size was too small to permit small carabids to escape, allowed free drainage and was too tough for large carabids to bite through. The sealant formed an effective bed for the gauze though, after some time, it would peel off the smooth base of the pot. It was found in the field that the pots would normally last about two months whilst the pitfalls themselves lasted indefinately and only needed to be replaced when broken by extraneous bodies such as tractors.

The traps were buried in the ground so that the soil was level

Figure 2.1a: Pitfall Trap

9cm

11cm

Glass pitfall

Wire mesh

Plastic insert

Figure 2.1b: Gutter Trap

Wire mesh

Gutter

8.5cm

Plastic cups
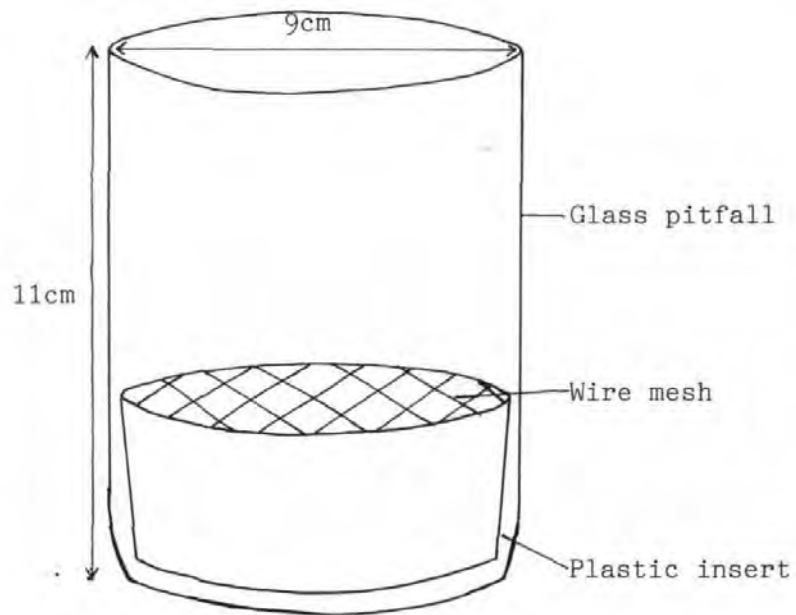
Collecting cup
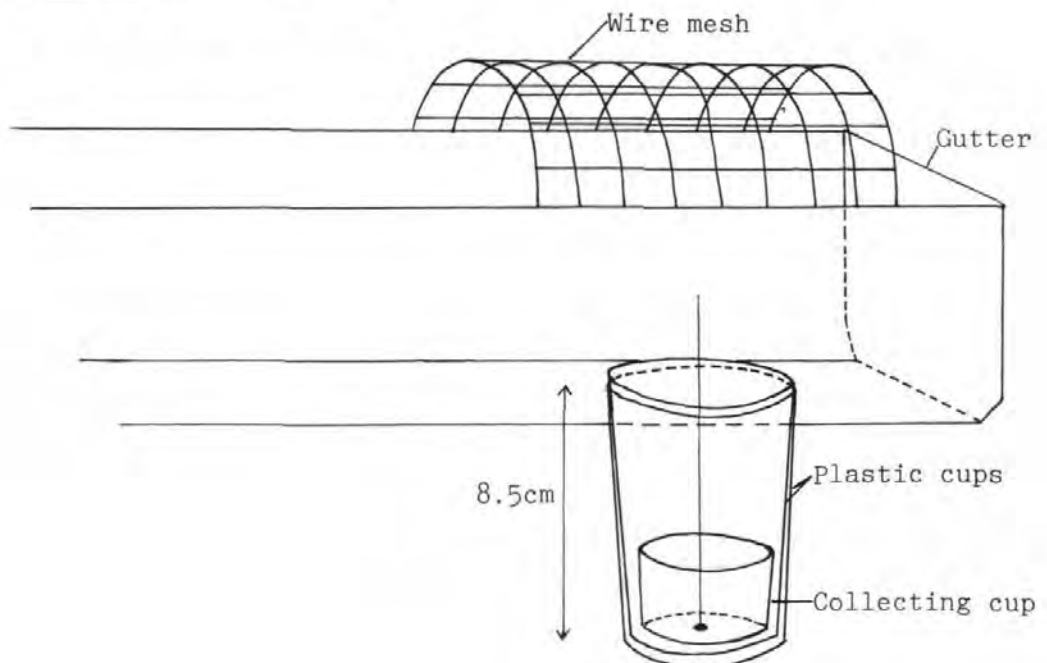
Figure 2.2a: Pitfall in field

Figure 2.2b: Pitfall with protective roof

with the rim of the glass (Fig. 2.2a). Any vegetation immediately in the vicinity was removed and the trap was reburied whenever necessary. The plastic insert allowed the catch to be removed without disturbing the pitfall. In order to prevent predation by birds or other animals a piece of galvanised steel mesh, with 2.5cm square holes, was placed inside the pitfall so that it rested on the top of the plastic insert (Fig. 2.1a). This could easily be removed to collect the catch but did not interfere with access to the pitfall itself. Although this arrangement normally appeared to prevent any loss, at one site (Rumleigh in 1985) it was insufficient. Here there was very heavy predation for a period by a particularly persistant and ingenious predator (probably magpies, <u>Pica pica</u>) and it was necessary to protect the traps with a sqaure shaped roof of clear perspex. This was a 15x15cm, and was supported about 10cm above the ground by tent pegs (Fig. 2.2b).

At each site the pitfalls were placed in a regular grid whose dimensions varied. Details are given in section 3.1.

Gutter Traps: Also known as strip traps these are equivalent to elongated pitfalls. The basic trap is based on one described by Luff (1975). They consisted of a 1m length of Bartol square section plastic guttering, shown in Fig. (2.1b). The dimensions were 11cm wide and 5cm deep, with a small lip along the sides, and it was made from black U.P.V.C. At one end a 5cm diam. hole was cut under which was fixed a container made from 2 plastic cups. Each of these had a 7cm diam. at the top, tapering towards the base, and was 8.5cm deep. The outer of the cups had a 2cm hole cut in the base, whilst the inner had the base completely removed. The inner cup provided strength and allowed a third cup, cut so that it was only

Figure 2.3a: Gutter trap, detail

Figure 2.3b: Gutter trap in the field

3cm deep,to fit closely inside the other two. The two cups were fixed to the base of the guttering by silicone sealant. The third cup was used to collect and remove carabids caught in the trap, drainage holes were cut in the bottom and covered with a piece of Simonyl N800 nylon mesh. Its removal was facilitated by a piece of stiff wire passed through the base and forming a handle.

The ends of the guttering were sealed using the standard end pieces produced by Bartol. Since the traps were produced from 3m lengths of guttering there was sometimes a small gap between the end of the gutter and the end seal, forming a crevice up which carabids might escape. This was prevented by fixing a small rectangular piece of clear plastic above the area, forming a wide lip.

As with the pitfalls a piece of steel mesh was used to prevent predation. This was formed from a rectangular piece (15x12.5cm) bent to form a roof over the collecting cup in the gutter (Fig. 2.3a). This normally rested under the lip of guttering and provided no obstacle to beetles in the trap and only a small obstruction to those on the surface.

At Rumleigh in 1985 predators learnt to remove the mesh and pull out the collecting cup and so modifications were necessary. The mesh was fixed to the ground with tent pegs, the sides of the mesh were cut and bent down towards the bottom of the gutter (preventing predators from getting underneath) and collecting cups without handles were used.

The gutter traps were buried in the soil so that this was level with the lip of the trap. Usually they were placed around the edge of the site (Fig. 2.3b).

At all times both types of trap were used without any preservatives, allowing live capture and subsequent release. Predation inside the traps was rarely a problem, and remains could be identified whenever necessary. For most of the period sites were visited three times a week (Monday, Wednesday, Friday), in the morning. The actual dates and number of collections are given in the relevent results sections.

Maintenance of carabids in the laboratory

During the project beetles needed to be maintained alive in the lab for identification, mark and release or for use in behavioural experiments. The majority were kept in a 10°c constant temperature room in plastic containers of various sizes, with damp tissue paper. They were fed on petfood (tinned dog or cat meat), no preference ever being found for any particular brand or flavour.

Carabids being used in behavioural experiments were kept in a 20°c constant room with a 16h/8h light/dark regime, but otherwise under the same conditions as the others.

Marking Techniques

A large number of studies have used marking of carabids in order to estimate population densities or obtain information on dispersal rates and directions. Different techniques have been used, ranging from paints to mutilation and individual marking by pitting the elytra. Petroleum based glossy dopes have been used (Greenslade 1964b, Pollard 1968) lasting for a few weeks to up to eight months, depending on the species, and Mitchell (1963b) used oil paint. All these authors state that there were no toxic effects of the paint, though Greenslade found that there was an effect of marking and

releasing, with an increase in activity for a short period after release. Penney (1966) marked N. brevicollis by clipping off the corners of the elytra whilst Lenski (1982) individually marked two species of Carabus by clipping off a combination of the 12 tarsal claws and recording sex.

Beetles can also be permanently marked by branding a pattern of holes in the elytra (Ericson 1977, Rijnsdorp 1980) or on the pronotal margin (Luff 1980). None of these studies found any effect of marking. A final method was adopted by Baars (1979) who marked carabids with a radio-active label allowing them to be found in the field and their dispersal monitored. The drawback of the technique is that the beetles are killed after a number of weeks.

Southwood (1978) states that any marking technique should not affect the longevity or behaviour of the individual. Although this is obviously important if the marking is being carried out in order to estimate population density, it is equally desirable if the aim is to study dispersal of the animal. Checks in the effect of marking can be made by comparing time and displacement to first recapture with those to the second and subsequent captures, similar to Greenslade (1964b). The effects on mortality can be assessed by comparing marked and unmarked individuals.

In this study carabids were marked using either paint or by drilling small pits in the elytra.

Marking with paint: A number of different paints were tried (acrylic, nail varnishes, enamel) but the most effective was found to be enamel. Acrylic proved difficult to apply and nail varnish flaked off in a few days and seems to be only available in a wide variety of shades of pink. Enamel paint is easily obtained in a range of colours and tests (Section 4.2) showed that it could remain on the beetle for

many weeks and possibly months.

Individuals to be marked were fixed by the thorax in strips of plasticine in order to immobilize them. The elytra were then completely coated with paint using a fine brush. A single coat was used unless the beetles were being marked with flourescent paint, which requires a white undercoat (Fig. 2.4a). Painting was carried out in deep plastic trays (16cm diam., 6cm deep) and up to 20 individuals could be marked at the same time. The paint was allowed to dry slightly before the beetles were released from the plasticine. With large species, such as P. melanarius, it was found necessary to further retain the beetles with a small strip of plasticine on top of the pronotum. Without this individuals would escape rapidly after marking and become stuck to the tray by the wet paint, they also showed an occasional and disturbing propensity to eat individuals which could not succeed in extricating themselves.

Beetles were all returned to the lab for marking and were then kept overnight before release. They were kept in a $10^{o}c$ constant temperature room and fed. This provided a chance to recover from any possible short-term trauma due to the marking.

Marking Individually: This was the predominant technique as more information can be gained by this method. Murdoch (1963) developed a system whereby marks in different striae signified different numbers of units, tens or hundreds and this was used by Ericson (1977) and Rijnsdorp (1980). The system adopted in this project was different as it proved difficult to make small enough marks. A modelling drill was used with a dentist's drill bit to abrade small parts of the elytra according to a set pattern (Fig. 2.5). Each beetle then had a unique set.

As when being painted each beetle was held in plasticine for

Figure 2.4a: Painted H. rufipes at Rumleigh

Figure 2.4b: Marked P. melanarius in pitfall, Staddon Heights 1985

marking, though a large block was used and each done individually. The process appeared to do no harm to the carabids and only exceptionally were the elytra drilled through entirely. The beetles were then kept overnight and fed before being released. Although sex was recorded it was not treated as an identification mark, so each pattern was used only once.

These beetles were marked permantly and could easily be recognised in the field with little possibility of confusion. On a very few occasions individuals were found which could have lost marks (through losing part of the elytra) and these were discarded unless identification could be guaranteed through lack of beetles with similar marks, combined with gender. Fig. (2.4b) shows recaptured carabids in the field. Although there are a relatively limited number of marks provided by the system marked individuals were difficult to miss and could easily be recognised in poor light or when covered with mud. At no time were insufficient marks available.

With practice it was possible to mark up to 60 inds/hour. Although a number of different species were involved it would be difficult to mark species smaller than N. brevicollis and it is impossible to use beetles with soft or thin elytra (such as Agonum dorsale) or callow adults.

Marked carabids were released from a specific point, usually in the centre of the grid of pitfalls. Those that were recaptured were released near the point at which they were trapped, around 30cm away from the trap.

Identification of Carabids

As far as possible all adult carabids were identified in the

field and immediately released unless needed for marking or other

purpose. All the results were entered on pre-prepared sheets. Any

new species or member of a difficult genus (e.g. Amara) were returned

to the lab. Carabids were identified using Lindroth (1974). If there

was any doubt about the species then it was checked against a

comprehensive collection, the Keys collection, in Plymouth City

Museum.

Figure 2.5; Individual marks, positions on elytra

To increase the number
marked the pattern is
repeated with an extra
pit at the position
marked X in the diagram
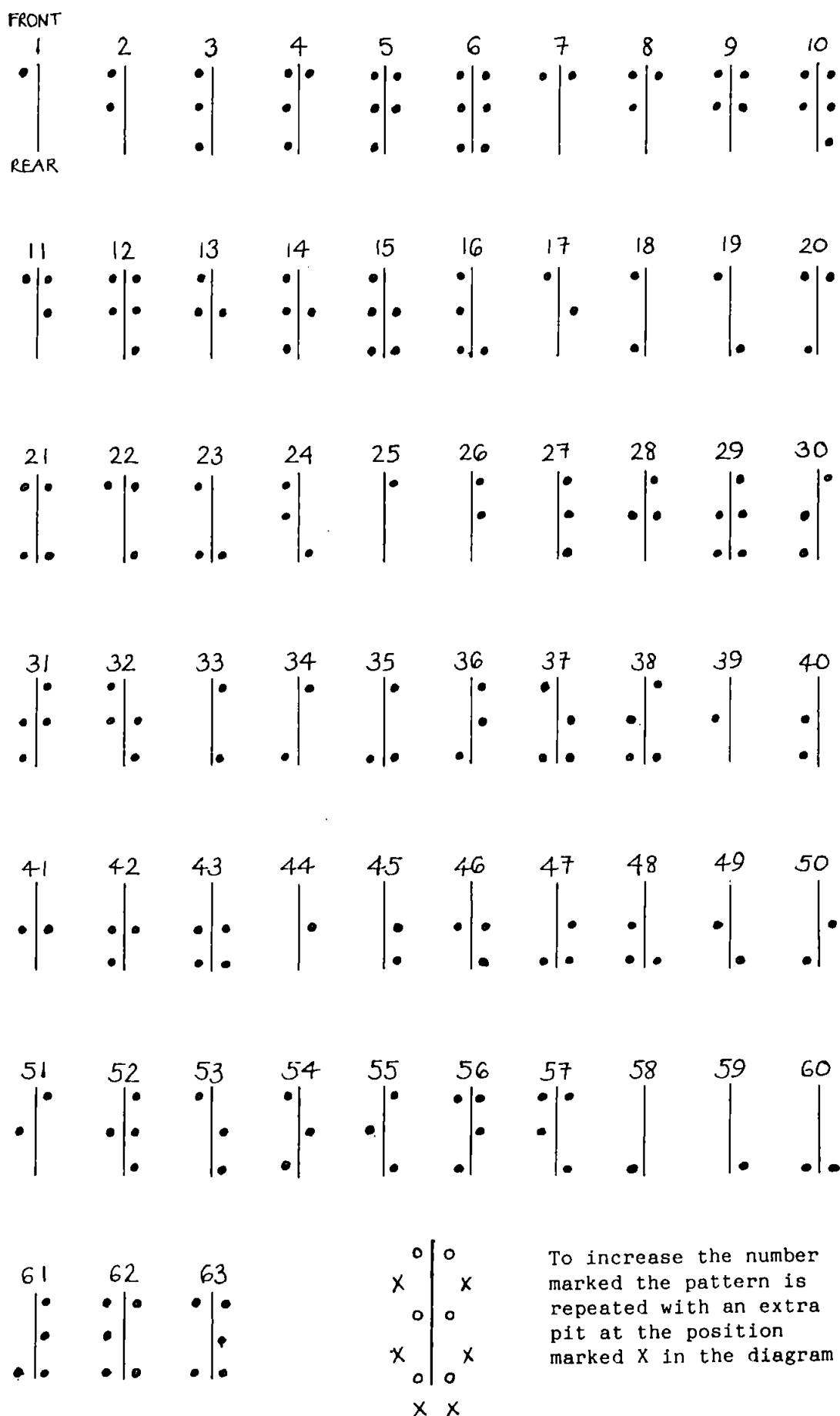
3.1 Field Sites

Field work was carried out at a number of different sites over the three years of the project. At Battisborough Cross and in two fields at Staddon Heights grids of traps were used to provide information about carabid distributions and temporal changes. At Rumleigh, Bere Alston, a large scale barrier plot allowed more controlled experiments involving mark/recapture techniques, whilst at Skardon Place, Plymouth, a small scale barrier plot was used in testing trapping and marking efficiency. Details of the different sites are as follows;

Battisborough Cross: Grid ref SX598483 Fig. 3.1

This site was situated some 13 miles from the Polytechnic and consisted of a large 7ha field, used as a market garden to grow different varieties of brassicas. These were grown mainly for human consumption and had been cultivated at the site continuously for at least the previous 15 years. Fig. (3.1) shows that the field was divided up into smaller areas by a number of tracks, allowing access for tractors.

The field was surrounded by a hedge bank, approximately 1.5m high with hawthorn bushes (Crataegus monogyna) growing on the top in places (Figs. 3.2a, 3.2b). Vegetation growing at the base of the hedge along the southern edge of the field was cut back at intervals by the farmer. However along the eastern hedge there was a strong growth of plants, mainly nettles (Urtica dioica), brambles (Rubus fruticosus) and Bracken (Pteridium aquilinum). The fields surrounding the site were mainly permanent pasture, though in 1984 cereals were grown in a small field to the east.

Figure 3.1: Battisborough Cross

Pasture

Pasture

100m
SCALE
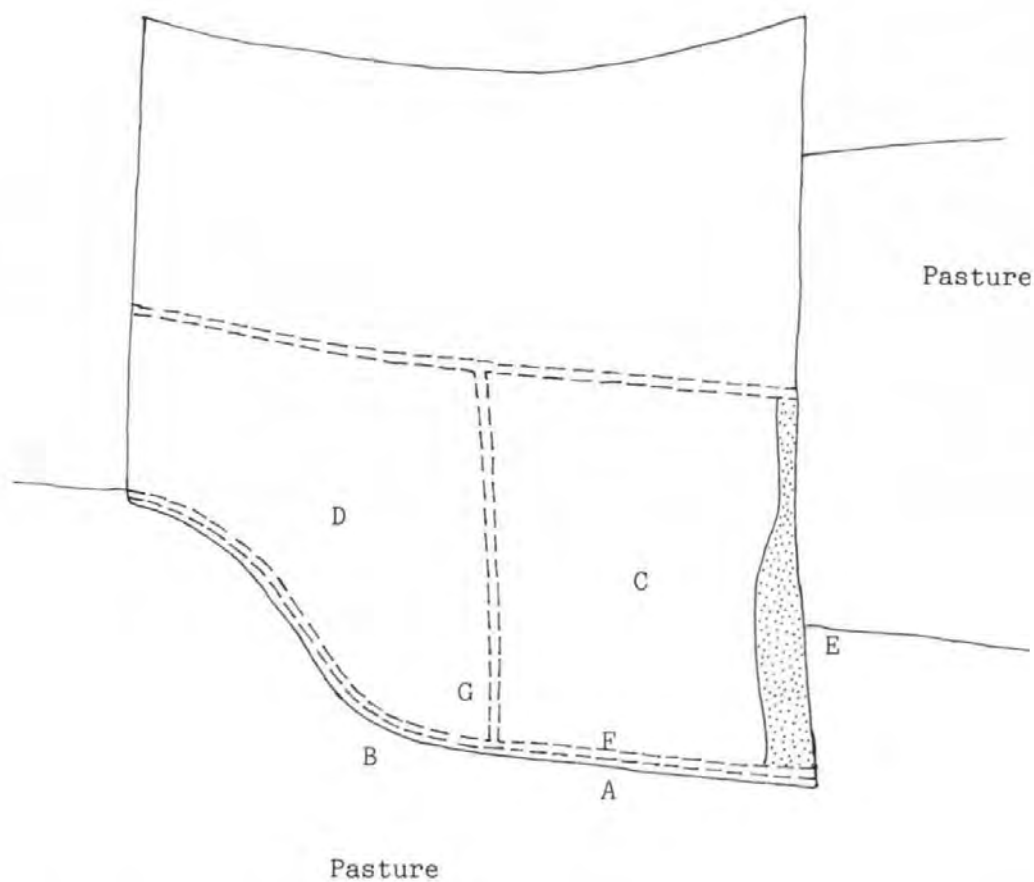
Key: A; Cabbage hedge — CH
       B; Fallow hedge — FH
       C; Cabbage field — CF
       D; Fallow field — FF
       E; Edge hedge   — EH
       F; Cabbage edge — CE (CG)
       G; Fallow path   — FP

Figure 3.2a: View of Cabbage Hedge

Figure 3.2b: View of Fallow Hedge

<u>Table 3.1</u>:

Trapping dates, Battisborough Cross 1983

Name	Type*	No.	Date in	Date out
Cabbage Hedge	P	5	6/4	1984
Cabbage 0m	P	5	6/4	17/6
Cabbage 10m	P	5	6/4	17/6
Cabbage 20m	P	5	6/4	17/6
Cabbage 50m	P	5	6/4	24/6
Fallow Hedge	P	5	6/4	1984
Fallow 0m	P	5	14/4	4/5
Fallow 10m	P	5	14/4	4/5
Fallow 20m	P	5	14/4	4/5
Cabbage Edge	G	5	22/7	1984
Fallow Path	G	3	1/8	1984

Trapping dates, Battisborough Cross 1984

Name	Type*	No.	Date in	Date out
Cabbage Hedge	P	5	1983	7/9
Cabbage Edge	G	5	1983	6/8
Fallow Hedge	P	5	1983	7/9
Edge Hedge	P	5	5/4	7/9
Grass Edge	G	5	23/2	2/4
Fallow Path	G	3	1983	9/4
Cabbage 5m	P	5	16/7	6/8
Cabbage 10m	P	5	16/7	6/8
Cabbage 15m	P	5	23/7	6/8

* P- Pitfall
  G - Gutter trap

Despite the continual growth of brassicas there were no serious pest problems during the period in which the site was used. Seedlings were transplanted in peat blocks from glasshouses and pesticides were applied before planting in the field. Insecticides were rarely used as sprays on the crop and never (as far as is known) during the period of study.

The intention at this site was to determine which carabid species were common in the area and to identify any patterns of movement, particularly in relation to the field boundaries.

Trapping was started 8/4/1983 and terminated 7/9/1984, occurring continuously in the hedgebanks. A number of different parts of the field were used, fitting in with the farmer's cultivation. Table (3.1) shows the dates over which trapping occurred during the two years. There were a number of problems with the placement of pitfalls at the site, mostly due to the exceptionally dry summers which prevented the farmer from planting out crops.

In 1983 grid of pitfalls provided information about movement of beetles away from the hedge and, later in the summer, gutter traps were placed around the edge of the site. In the subsequent year trapping continued at the field edges and in the boundaries but, due to the dry weather, it was not possible to place traps in the fields themselves. In July 1984 the field was sold at very short notice and cultivation of brassicas ceased, all traps were subsequently removed.

During the two years a total of 41 different carabid species were found (Tables 3.2, 3.3), the most abundant being P. melanarius, N. brevicollis, B. lampros and H. rufipes.

Staddon Heights: Grid ref SX504513 Figs. 3.3, 3.5

Two different fields, one each in 1984 and 1985, were used, both

Figure 3.3: Staddon Heights 1984

Cereals

A; 1st area
B; 2nd area

Pasture

A

B

50 m
SCALE

Pasture

Figure 3.5: Staddon Heights 1985

Cereals

West Gutters

Pasture

North Gutters

20m
SCALE
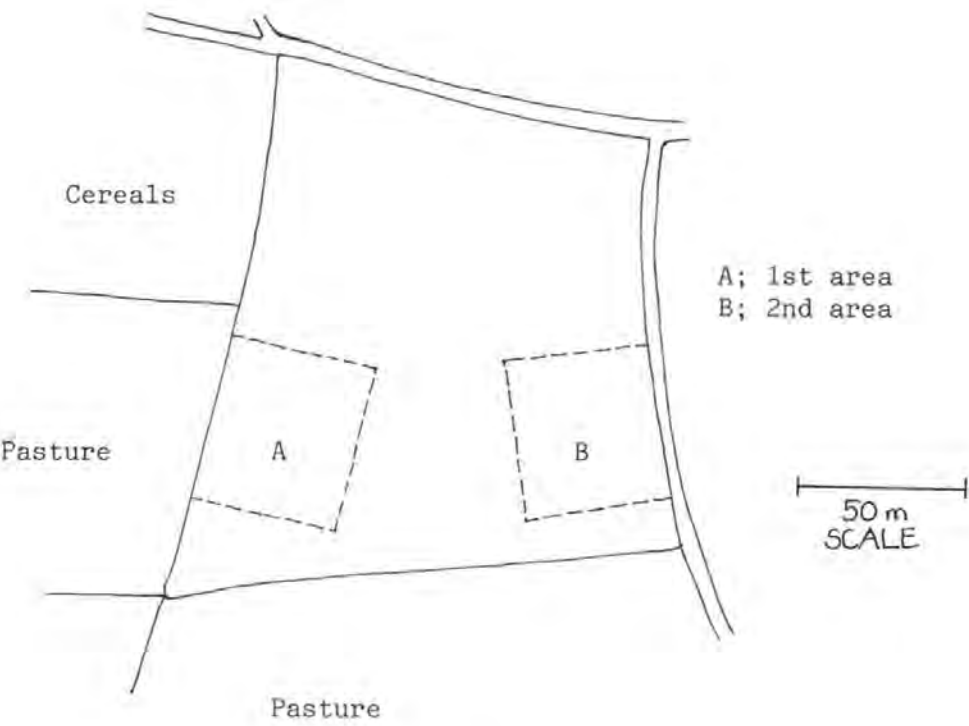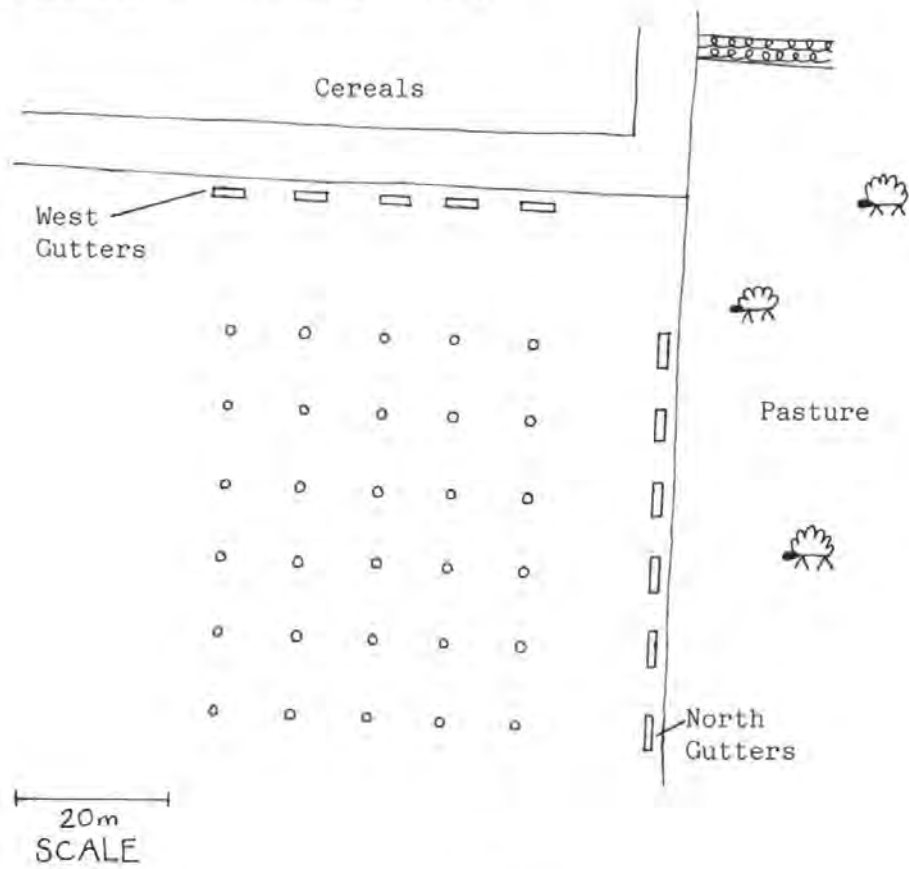
Figure 3.4a: Staddon Heights, 1st area of site

Figure 3.4b: Staddon Heights, 2nd area of site

parts of the same farm. Manor Court Farm had a mixture of cereals and pasture for sheep and cattle. Each year the farmer planted one field with brassicas (swedes in both years of the study) primarily for human consumption but also as fodder. The crop was normally planted in early summer, for harvesting early in the following year.

The field studied in 1984 was about 1.6ha (Fig. 3.3) on the side of a small valley. It sloped in a south-westerly direction and was bordered by roads to the north and east. Most of the field was surrounded by a wire fence but a 100m section was bordered by an overgrown hedgebank which contained some large trees. The fields surrounding the site were all permanent pasture, except for a cereal crop, situated on half the western edge.

Before 1984 the field itself had been permanent pasture "in living memory" and so the swedes planted formed the first crop. Although intended for human consumption, the crop was not sprayed with insecticide. However it did become seriously affected by mildew and was sprayed with a fungicide in September (15/9/1984). In November it was decided to use the crop for fodder and so cattle were allowed into a strip, which was moved progressively across from the western edge.

The first traps were enplaced 23/7/84 along the hedge, in the south-western area of the field (Fig. 3.4a). Owing to the extremely hard soil it proved necessary to put in further trap lines at later dates. The final grid consisted of 40 traps in 8 lines each 5m apart, each line made up of 5 traps each 10m apart. Trapping continued until the end of November when the introduction of stock meant that the pitfalls were moved to different area at the top of the field. The grid was then based along the wire fence, but with the same configuration as before (Fig. 3.4b). Sampling was terminated early in 1985.

Figure 3.6a: Staddon Heights 1985, view near North Gutters

Figure 3.6b: Staddon Heights 1985, in centre of field

In the field 26 different carabids were found with <u>N. brevicollis</u> and <u>P. melanarius</u> being the most abundant, followed by <u>T. quadristriatus</u> and <u>H. rufipes</u> (Table 3.4).

The following year, 1985, a field some 600m to the south-west was used (Fig. 3.5). The site sloped gently to the east but was flat in the area used for trapping. Unlike previous sites there was no hedge, the field being surrounded by a wire fence. On three sides there was pasture with sheep and on the remaining side there was a wheat field separated by a track and low mound.

The swede crop was planted in early summer and the grid of pitfalls was put in position 22/8/85. This consisted of 30 pitfalls each 10m apart forming a 6x5 grid, with the first traps 20m from the field edge. Gutter traps were placed along two edges of the site, corresponding with the lines of pitfalls (Fig. 3.5). Sampling was completed on 8/11/85. Figs. (3.6a, 3.6b) show the area where traps were placed. These photographs were taken in late August and the difference in the swede growth in the two areas should be noted.

The species found at the site are shown in Table (3.5). The most common were <u>P. melanarius</u> and <u>N. brevicollis</u>, although <u>C. fuscipes</u> and <u>T. quadristriatus</u> were also caught in large numbers.

Rumleigh Experimental Station: Grid ref SX446683 Fig. 3.7

The Polytechnic's experimental station covers 3.6ha and is 14 miles from Plymouth. A variety of plants are grown and plots are available for experimental purposes. The surrounding area includes woods and market gardens with an emphasis on strawberries. The majority of the was work was carried out in a 25x55m plot planted with Primo cabbages (Figs. 3.8a, 3.8b). This was surrounded by a polythene barrier to prevent the movement of beetles in or out of the plot. The

Figure 3.7: Rumleigh 1985, Layout of plot

Barrier

Gutters

Pitfalls

X; Release point

10 m
SCALE
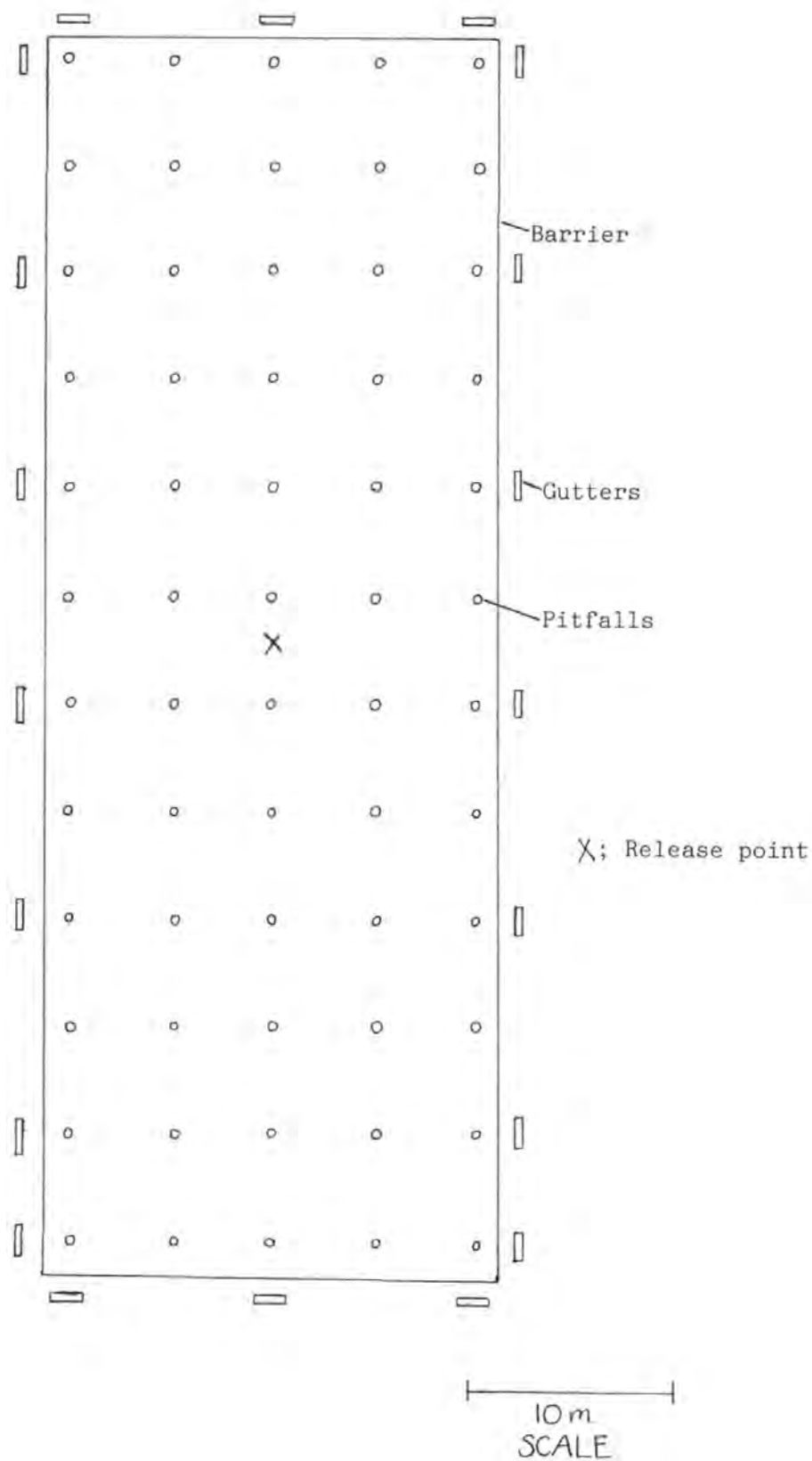
Figure 3.8a: Rumleigh 1985, inside plot

Figure 3.8b: Rumleigh 1985, general view outside plot

barrier was 50cm high, buried to a depth of 20cm with a lip extending under the ground about 20cm into the plot. The polythene was supported by wire strung between wooden stakes, situated at 3m intervals. Wooden slats were used to fix the polythene to the stakes (Fig. 9.a), and the tops of these were covered with sellotape to prevent carabids climbing out. Although a double thickness of plastic was used, movement of the barrier in the wind, together with the very stony soil, caused tears in the polythene at the soil surface. These were sealed on both sides using heavy duty sellotape.

The cabbages were grown from seeds sown in the plot but the dry spring prevented early germination. Rows of cabbage were 30cm apart and as the plants grew thinning took place so that there was a similar distance between cabbages. No pesticides were sprayed inside the plot but weeds grew in great profusion. Until the cabbages grew sufficiently to withstand herbicide weeding was carried by hand, but after this paraquat was applied between the rows and at the base of the barrier.

Pitfalls were put in on 18/5/85 and eventually formed a grid of 60 traps (5x12) each 5m apart (Fig. 3.7). They were all placed between the rows of cabbage. On the outside of the plot 20 gutter traps were placed at 10m (7 on each of the longer sides and 3 on the shorter).

As mentioned in Section 2.1, the anti-predator protection was inadequate at this site and modifications were made. Very high mortality, caused by the extremely dry hot weather, occurred in the traps and in an attempt to reduce this damp paper was placed in the pitfalls. Unfortunately predators learnt to pull the paper, together with the mesh preventing access, from the pitfalls and so fed on any trapped carabids. Having achieved this they also started to remove

Figure 3.9a: Rumleigh 1985, detail of barrier

Figure 3.9b: Skardon Place

the cups from the gutter traps and all variations (such as placing large stones in the traps to provide shelter) were instantly thwarted. This led to the modifications described earlier.

The were a number of differences in the fauna at Rumleigh. P. melanarius and H. rufipes were the most abundant but there were also large numbers of P. cupreus and P. madidus. Table (3.6) shows the 26 different species found.

Skardon Place: Grid ref SX 482553 Fig. 3.9a

A small, walled garden (0.1ha) close to the Polytechnic provided an area were experiments could be carried out in outdoor conditions but which were easily controlled. The site was used primarily for growing plants for research and there are a number of glasshouses and various flower beds. Small plots were used with pitfall and gutter traps.

The main plot was 3x3m in size and was surrounded by a polythene barrier, similar to the one at Rumleigh. A single piece of polythene was used, suspended by wire from wooden stakes at 2.5m intervals. Owing to the small scale the polythene was fixed to the wire with large staples and there was a generous overhang, preventing escape.

The plot was installed on 12/4/84 and used to test various different types of marking scheme and also the effectiveness of traps. Before this period the plot had been used to grow plaintains (Plantago spp.) and these were left in 1984 but thinned to provide some cover, the dry weather preventing cabbages from being planted.

In 1985 72 cabbages were planted in the plot, with 30cm between each plant. These were grown in a greenhouse until the seedlings were large enough to be transplanted to the plot. Five pitfalls were used (one in the centre and one in the middle of each side) and a number of

marked carabids were released. At all times there were various traps outside this plot.

Almost all the beetles used here were introduced from other sites but there was an indigenous population of carabids. Species found included <u>N. brevicollis</u>, <u>Amara aenea</u>, <u>A. ovata</u> and <u>Asaphidion flavipes</u>. In 1985 <u>H. rufipes</u> were found, probably originating from those introduced the previous year.

Table 3.2:

Battisborough Cross 1983: List of species found and number of individuals

SPECIES	Cabbage hedge	Fallow hedge	Cabbage 0m	Cabbage 10m	Cabbage 20m	Cabbage 50m	Cabbage edge (G)	Field path (G)	Total
Leistus ferrugineus	1								1
L. fulvibarbus	1	5		1			3		10
Nebria brevicollis	239	373	56	122	96	60	517	671	2134
Notiophilus biguttatus	2		6	1	7	6	11	14	47
Loricera pilicornis	22	24	27	15	20	8	40	7	164
T. quadristriatus	26	22		3	2	1	15	4	73
Asaphidion flavipes						1			1
Bembidion lampros	59	62	55	60	64	79	228	103	770
B. quadrimaculatum						1			1
Pterostichus cupreus	2		4				7	5	18
P. madidus	4	1			1		59	12	77
P. melanarius	32	14	8	38	12	5	554	210	873
P. niger	15	11					8	2	36
P. strenuus	9	7	3		5	1	2		27
P. vernalis							1	2	3
Calathus fuscipes	2						9	4	15
C. melanocephalus							1		1
Synuchus nivalis							1		1
Agonum dorsale	34	26	18	48	55	33	15	15	244
A. muelleri	1	1	55	23	52	32	2		166
Amara aenea		3	24	15	26	19	44	22	152
A. apricaria							7		7
A. bifrons							1		1
A. communis							2		2
A. familiaris						1		1	2
A. ovata			5	11	5	3	36	5	65
A. plebeja	3		2	3	2		61	7	78
Harpalus aeneus			1				20	1	22
H. rufipes	19	2	4	2	5	2	515	61	610
Bradycellus verbasci							1		1
Badister bipustulatus	2				1				1

Table 3.3:

Battisborough Cross 1984: List of species found, with number of individuals

SPECIES	Cabbage hedge	Fallow hedge	Edge hedge	Cabbage edge (G)	Fallow path (G)	Cabbage field	Edge (G)	Total
Leistus ferrugineus	3		2					5
L. fulvibarbus	7	3	5				2	17
L. spinibarbis	1							1
Nebria brevicollis	47	214	31	293	39		11	635
Notiophilus biguttatus		3		18	5	1	16	43
Loricera pilicornis		4		3		2	1	10
T. quadristriatus	35	24	8	22	6		78	173
T. obtusus	37	2	4	4				47
Asaphidion flavipes		1						1
Bembidion lampros	35	42	21	190	4	203	18	292
b. lunulatum		2						2
B. obtusum				4				4
B. quadrimaculatum						22		22
Pterostichus cupreus	1	4	1	40		13		59
P. madidus	1	1		6		3		11
P. melanarius	4	17	21	420		402		864
P. niger	11	13	14					41
P. strenuus	9	13	35	27			1	85
P. vernalis				2				2
Calathus fuscipes						1		1
C. melanocephalus	1							1
Agonum dorsale	23	49	7	28				107
A. muelleri	1	4		51		39	3	98
Amara aenea	2	1	9	152	4		44	212
A. communis			4	9				13
A. equestris				1				1
A. familiaris		7	1	36		3		47
A. lunicollis			1	1				2
A. ovata	2		122	75	1	23	1	224
A. plebeja		3		103		5	1	112
Harpalus aeneus				8		4		12
H. rufipes	1	5	2	228		208		444
Bradycellus verbasci	1		1					2
Acupalpus meridianus						1		1
Badister bipustulatus	13	4	22	5				44
Demetrias atricapillus	5	5	4					14
Dromius melanocephalus		1						1

Table 3.4:

Staddon Heights 1984; List of carabid species, with number of individuals

SPECIES	Hedge	Edge	Field	Total
Cychrus caraboides			1	1
Leistus ferrugineus	4			4
L. fulvibarbis	1		1	2
Nebria brevicollis	757	562	2321	3640
Notiophilus biguttatus	13		1	14
Loricera pilicornis	1			1
Trechus quadristriatus	36	69	328	433
Bemdibion lampros	19	2	12	33
Pterostichus cupreus	5	3	29	72
P. madidus	6	3	63	72
P. melanarius	171	282	1546	1999
P. strenuus	2		2	4
Abax parallelopipedus	1		1	2
Calathus fuscipes	18	3	3	24
C. melanocephalus	5	3		8
Agonum dorsale	6	2	2	10
A. muelleri	2	7		9
Amara aenea		1	27	28
A. aulica	2	3		5
A. bifrons	4			4
A. familiaris		1		1
A. ovata	2			2
A. plebeja	1	6	9	16
Harpalus aenea	1			1
H. rufipes	73	20	39	132
Bradycellus verbasci	4			4

Table 3.5:

Staddon Heights 1985; list of carabid species, with number of individuals

SPECIES	Field	North gutters	West gutters	Total
Nebria brevicollis	201	314	138	653
Notiophilus biguttatus	21	1		22
Loricera pilicornis	1	5	2	8
Trechus quadristriatus	358	40	25	423
Bembidion lampros	20	12	2	34
B. quadrimaculatum			1	1
Pterostichus cupreus	3	1	3	7
P. madidus		5	5	10
P. melanarius	1240	1231	329	2800
Calathus fuscipes	16	18	13	47
C. melanocephalus	88	560	294	942
C. piceus	1			1
Agonum dorsale	3	4	5	12
A. muelleri			3	3
Amara aenea	175	94	85	354
A. bifrons			1	1
A. ovata	7		3	10
A. plebeja		1		1
Harpalus aeneus	16	38	24	78
Harpalus rufipes	2	22	95	119

Table 3.6:

Rumleigh 1985; List of carabid species, with number of individuals

SPECIES	Pitfalls	Gutters	Total
Carabus violaceus	21	5	26
Nebria brevicollis	13	45	58
Notiophilus biguttatus	40	12	52
Cychrus caraboides		1	1
Loricera pilicornis	2	2	4
Trechus quadristriatus	134	18	152
Bembidion lampros	64	74	138
B. quadrimaculatum	65	33	98
Pterostichus cupreus	760	484	1244
P. madidus	324	501	825
P. melanarius	949	1908	2857
P. niger	1	1	2
P. strennuus	1	20	21
P. vernalis		2	2
Agonum dorsale	1	1	2
A. muelleri	8	22	30
Amara aenea	4	30	34
A. communis		1	1
A. familiaris	8	23	31
A. ovata	39	26	65
A. plebeja		8	8
Harpalus aenea	31	183	214
H. rufipes	712	1717	2429
Clivina fossor	2		2
Badister bipunctulatus	1	5	6
Bradycellus verbasci		1	1

4. Pitfall trapping- results and discussion.

A large amount of information was obtained from the carabids caught in the traps. Various aspects of the results are covered in the following sections, which are arranged in biological themes. They include the overall habitat preferences of the different species found, seasonal changes in numbers, the effect of meteorological factors and the distribution of the carabids within the fields.

4.1 Habitats of the different species

There are a number of carabids which are associated with agricultural habitats in Europe (Thiele 1977). These include all the species which were found in large numbers at the sites studied during this project. In comparing the sites it must be remembered that trapping occurred at different times of the year and that the use of pitfall and gutter traps also caused differences, particularly in the relative proportions of the various different species caught. With this in mind Table (4.1) shows the five most abundant species at each site. P. melanarius occupies the first or second position at all times, whilst N. brevicollis is similarly placed with the exception of Rumleigh, where sampling occured largely outside this species' period of activity.

The three species H. rufipes, B. lampros and T. quadristriatus are also common at each site. The difference between B. lampros (common at Battisborough Cross) and T. quadristriatus (common at Staddon Heights) may be due to real habitat requirements. Mitchell (1963a) showed that the first species prefers warm, open areas whilst the second seeks shady areas under the crop. However B.lampros was

Table 4.1:

The five most abundant species at each site

Battsbrgh 83	Battsbrgh 84	Staddon 84	Staddon 85	Rumleigh 85
N. brev	P. melana	N. brev	P. melana	P. melana
P. melana	N. brev	P. melana	N. brev	H. rufipes
B. lampros	H. rufipes	T. quad	T. quad	P. cupreus
H. rufipes	B. lampros	H. rufipes	A. aenea	P. madidus
A. dorsale	A. ovata	P. madidus	H. rufipes	H. aenea

Table 4.2:

Preferred zones of the different species

Hedge	Border	Mixed	Field
Leistus spp.	L. pilic.	N. brev.	P. cupreus
P. niger	P. strenuus	T. quad.	A. muelleri
T. obtusus		B. lampros	A. aenea
B. bipunct.		P. madidus	
D. atricap.		P. melana.	
		A. dorsale	
		A. ovata	
		H.rufipes	

mainly active in spring and summer whilst T. quadristriatus peaked

later in the autumn, so the difference may also be influenced by the

trapping periods (details of the seasonal changes are contained in

Section 4.2).

For those species which were captured less frequently there are

some large differences between the sites. Many of these are due to

changes in field boundaries, particularly hedges. A number of

different studies have shown the importance of these (Pollard 1968,

Wallin 1985, Lyngby and Nieslen 1981). The carabids can be

categorised according to their relationship with habitats surrounding

the fields. Species may be restricted to the boundaries, they may

inhabitat a 'border zone' which is under the influence of the

boundary, or may live in the field itself. Field species may have an

association with the boundaries (e.g. as overwintering sites), may be

active there but primarily found in the field, or may be almost

entirely restricted to the field. Table (4.2) classifies species

found during this project. The majority of species have their main

focus in the field but are also present in the boundaries,

particularly at certain times of the year. There is a large variation

between sites, explained below. The major distinction appears to be

between those species confined to hedgerows and those found in the

field and grassy borders.

Species confined largely to the hedgebank (P. niger Schaller,

Leistus spp., T. obtusus Erichson, Badister bipunctulatus Fab.,

Demetriatus atricappillus L.) were found only at Battisborough Cross

and the first Staddon Heights site (with the exception of two P. niger

at Rumleigh). These may be species which are primarily woodland

carabids and the hedge forms an area of suitable habitat. However

there is little interchange with the field itself. At Staddon Heights

two species normally associated with woodland were caught (Abax parrallelopipedus and Cychrus caraboides), and these were probably vagrants moving between the many areas of woodland around the site.

The majority of individuals belonged to species which inhabitated both the field and the boundaries. The relationships of these species will be discussed in more detail in a later section. However many of these carabids use the field edges as over-wintering sites. Finally there were a few species which were very rarely caught in the hedgebanks. Although caught in field and at the edge these species differed from the others since the were only occasionally active in the hedge. Over-wintering sites were probably in the field or in the grassy edges.

Many species were caught in numbers at all the areas sampled, and some of these had distributions which were highly variable. For instance A. ovata was normally caught almost entirely in the field, but in one part of the hedge at Battisborough Cross ('Edge Hedge' 1984) it was very frequent. Calathus fuscipes was very common at Staddon Heights in 1985, and C. melanocephalus was also found, this species preferring dry areas (Andersen 1982). The soil was very heavy clay and it was often extremely wet, thus it is possible that the populations of these two species at this site were associated with the adjoining pasture. The majority of C. fuscipes were captured in the gutters adjacent to these areas.

There are a number of differences between the distributions found in this study and those found in others. Lyngby & Nieslen (1981) found that T. quadristriatus and Notiophilus biguttatus were both shelterbelt species, though Pollard (1968) states that T. quadristriatus had no association with the hedge. The restriction of T. obtusus to hedgerows found by Pollard is supported by this

study. Lyngby & Nielsen found that <u>A. aenea</u>, <u>A. ovata</u> and <u>Loricera</u> pilicornis were field species, whislt this study found a similar distribution of <u>A. aenea</u>, but <u>A. ovata</u> and <u>L. pilicornis</u> were both found in large numbers in the hedgerow.

These differences illustrate the fact that carabids adapt their distributions according to a number of factors and may not be constant. Micro-climatic factors are likely to be most important and these vary greatly between crops and field boundaries. Thus species which have a particular distribution at one site may have very different distributions in other areas and broad categorisation of species should be approached with caution.

4.2 Seasonal Changes in Abundance.

There have been numerous studies on the annual cycles of carabids found in crop situations. As mentioned in Section 1.1, Thiele (1977) classifies different species according to their breeding season and the periods in which they are active. Figs. (4.1-4.26) show the seasonal changes for a number of carabid species at the sites used during this project. The same patterns described by other studies was found in this area, though activity extended later into the winter than has been found elsewhere. For each species there is a certain amount of variation between the different sites. Changes in numbers caught are due to a mixture of variations in density and activity, and activity itself depends on the beetle's physiological condition, the season and sex (Brunsting 1983). Superimposed on the seasonal scale changes caused by biological factors, are large differences between days, probably due to meteorological factors. The effects of temperature, rain and other such variables are described at the end of this section, but first the broad seasonal cycles are described. Each species is treated separately below, in order to facilitate search amongst the maze of figures these are all listed in a table on pg. 79. The figures are at the end of this section (pg. 80-108).

Bembidion lampros;

In the hedgerows activity started in the second week of April and continued until the end of September (Figs. 4.1, 4.7). There was a small amount of activity outside these times, particularly at Staddon Heights in both years when individuals were active until the end of November.

The species in a spring breeder (Mitchell 1963a) whose main

period of activity is in May (Mitchell 1963a, Jones 1979), activity in the late summer and autumn is due to newly emerged individuals. Jones (1979) in southern England and Andersen (1982) in south-eastern Sweden found very little activity in August and September, whilst at Battisborough Cross in 1983 there were large numbers caught in the gutter traps in late August and September, with a corresponding increase in the hedgebank. Previous to this there were few captures and this is possibly due to the hot, dry weather.

Agonum dorsale;

This species is another spring breeder, showing a peak of activity in the spring slightly later than B. lampros (at the beginning of May, Figs. 4.2, 4.8). There was very little activity early in the spring and at Battisborough Cross in 1984 there is a short marked peak in the catch in the hedgerow (Figs. 4.8a, 4.8c). In this it differs from B. lampros where individuals were caught at low levels for the whole summer. Relatively low numbers were found in the gutter traps at the site but the main period of activity is probably over towards the beginning of August. Individuals active in the autumn are those which have emerged the previous summer. Pollard (1968) found high levels of activity during May, decreasing during June and increasing again at the end of July and August. Jones (1979) found a similar pattern, though there was high activity in June and very little in August. The species has been shown to migrate away from hedges in the spring and return later (Pollard 1968). At Battisborough Cross in 1983 there was evidence for migration away from the hedge (Fig. 4.30, Section 4.5), but there was much lower activity later in the year.

It's relative, A. muelleri, appears to have a similar pattern of

activity (Fig. 4.12c) and is active for the same period.

Pterostichus cupreus;

Although only caught in large numbers at one site (Rumleigh 1985) the trapping there provides sufficient information for the species' annual cycle to be described. Like the previous carabid, this is a spring breeder, at Rumleigh large numbers were caught at the end of May and beginning of June (Figs. 4.16a,b). The numbers then dropped substantially from mid-June followed by a small increase in August, due mainly to teneral adults. From results before the set of pitfalls was complete it is apparent that activity started from the first week of May and peaked at the end of the month, as the final pitfalls were put in position. At Battisborough Cross in 1984 individuals were first caught in late April but peak in mid-June, before dropping rapidly in July (Fig. 4.10a).

At Rumleigh 1985 the numbers of males and females caught were recorded for both the pitfalls and gutter traps. During the period (from 24/6-21/8, with no records during the middle of July) a total of 90 males and 142 females (0.63:1) were caught. The ratios in the gutter traps and pitfall traps are similar (0.66:1 and 0.46:1). Owing to the low numbers caught after the beginning of June there is no evidence of any change in this ratio during the season.

Ericson (1979), trapping from the second week of May until the end of July in Sweden, found that numbers were low until the end of May, peaked the second week of June and very low numbers were caught in July. Thus activity in Devon would appear to start earlier and continue longer, as would be expected.

Nebria brevicollis;

N. brevicollis was captured throughout the year but clearly
showed the two peaks of activity found in previous studies (Greenslade
1964b, Penny 1966, Jones 1979). The spring peak occurred in early
followed by a rapid decline (Fig. 4.3), so that there was very little
activity in July and August. At Battisborough Cross the autumn
breeding activity peaked at the end of September and then appeared to
decrease (Figs. 4.3, 4.9) whilst Fig. (4.14b) shows that at Staddon
Heights in 1984 numbers increased until the end of October and then
continued at fairly high levels into December.

The timing of the activity was found to be similar to that shown
in other studies, particularly Williams (1959), though it appears to
be a higher level of activity continuing through from November to
early spring.

Pterostichus melanarius;

This species was found in large numbers at all sites. Although
some individuals were found in late April and early May most activity
did not commence until late July (Figs. 4.4, 4.10b, 4.17a,b, 4.22).
The beetles were then common until the end of September or early
October, only occasionally being found after this date.

As with P. cupreus the numbers of the two sexes were recorded,
though this was done at Staddon Heights in 1985 as well as at
Rumleigh. In total the were 747 males and 585 females (1.28:1) caught
at Rumleigh, there being no difference between the two different types
of trap (1.31:1 and 1.35:1). At Staddon Heights records were kept for
the whole period (26/8-8/11), with 555 males and 622 females being
caught (0.89:1). Apart from there being relatively more females at
Staddon Heights there was also a larger difference between the two

types of trap with the ratios on pitfall and gutters being 1.06:1 and 0.81:1 respectively.

Unlike P. cupreus it is possible to identify a pattern in the changing proportions, although there is obviously a certain amount of daily variation. At Rumleigh the proportion of males was highest in May and early July (1.72:1) and this decreases until early August (1.46:1) whilst towards the end of the trapping period the ratio was reversed and the mean after 14/8 was 0.86:1. This pattern is continued at Staddon Heights where at the end of August and early September the ratio was 2.02:1, steadily decreasing so that after the begining of October more females than males were found (the mean male/female ratio after 4/10/85 was 0.51:1). It is unclear whether these changes are due to changes in numbers or the relative activity of the sexes, although it is likely that both are involved. At Staddon Heights it does appear that females are active for longer than the males, in the pitfalls after mid-October only 7 males were caught compared with 30 females. The difference between the two traps is because in early September relatively more males were caught in the pitfalls. The difference in overall ratios between the two sites is probably caused by the different trapping, rather than any intrinsic differences between the two populations. Ericson (1978) suggested that male activity was higher in females than males during July, and that male activity increased at the end of the month, this will be discussed further in the section on mark and recapture.

Jones (1969) found a similar annual pattern of activity and, by dissecting females, showed that the early activity is due to beetles which have over-wintered, whilst the increase in July is caused by newly emerged individuals. Other studies on the species' temporal distribution (Ekbom.& Witkelius 1985, Andersen 1982, Wallin 1985) show

that the annual cycle in the same everywhere, though in Scandinavia activity may cease in August or early September.

Harpalus rufipes;

Although not found at all the sites in as large numbers as P. melanarius, this species has a similar a similar annual pattern of activity. The first beetles were caught in May and at Rumleigh in 1985 (Fig. 4.18a,b) there is a marked peak at the beginning of July. Activity continued until the end of September and after this numbers caught were lower than P. melanarius (figs 4.5, 4.23c). Luff (1980) found that H. rufipes had a longer period of activity than P. melanarius, from April until the end of October. Other studies (Jones 1979, Wallin 1985, Andersen 1892) have found that the periods of activity of the two species were closely similar. In this project P. melanarius was caught in larger numbers late in the season, during October until late November. This was particular true at Staddon Heights where quite large numbers of H. rufipes were captured in August and the beginning of September after which numbers dropped off rapidly, and none were found in October (Fig. 4.23c)

At Rumleigh in 1985 the ratio of males to females was 0.69:1 (513 males and 748 females). Although more variable than in previous species there is a suggestion of a pattern similar to P. melanarius. Although more females than males were caught on all but a few days, the ratio of males to females drops from 0.87:1 at the beginning of July to 0.51:1 after mid-August.

Luff (1980) and Jones (1969) found that newly emerged adults occurred at the end of July and early August, later than the corresponding date for the previous species.

Trechus quadristriatus;

Mitchell (1963) describes this species as an autumn breeder which continued activity through the winter but which was much less active than B. lampros in the summer months. Jones (1979) also found larger numbers in the autumn whilst in Scandinavia Andersen (1982) found that numbers usually peaked in August or late July with few caught later.

The activity in the winter can be seen at Battisborough Cross in 1984 (Fig. 4.11a) when individuals were caught from January onwards. Although numbers were low there is a peak in April and the catch in the hedge over the summer was similar to that of B. lampros (although numbers of B. lampros were much higher at the edge of the field). At Rumleigh in 1985 (Fig. 4.16c) the beetle was active in May and June but none were caught from mid-July until the end of August when there was a marked peak. At Staddon heights it occurred in variable numbers from the end of August until the end of November (Fig. 4.23a,b). Together with N. brevicollis it was the only species caught consistently in the winter months.

Amara aenea;

This was always the most abundant of the Amara species in the traps at all the different sites. Figs. (4.12a, 4.25) show that it had a very extended period of activity with the first individuals being caught in late January and activity continuing into November. The numbers caught were highest during the summer, apparently peaking in April and May, but catch was still high during October (Staddon Heights 1985).

Although data on other Amara species was much less complete, Figs. (4.11, 4.12a) suggest that A. aenea had a longer period of activity than the other species found. Both A. plebeja and A. ovata

were only found in the traps from May onwards and did not peak until June.

The results show that carabids have a similar annual pattern to that found elsewhere. The relatively mild winters probably allow activity to continue longer in many years, though whether this has any effect on over-winter mortatility is unknown.

The figures of the seasonal changes follow. They contain some figures of meteorological factors, which are discussed in the next section.

List of species and figures

Fallow Hedge

Fallow Path

Cabbage Hedge

Cabbage Edge

Figure 4.2: Agonum dorsale, Battisborough Cross 1983
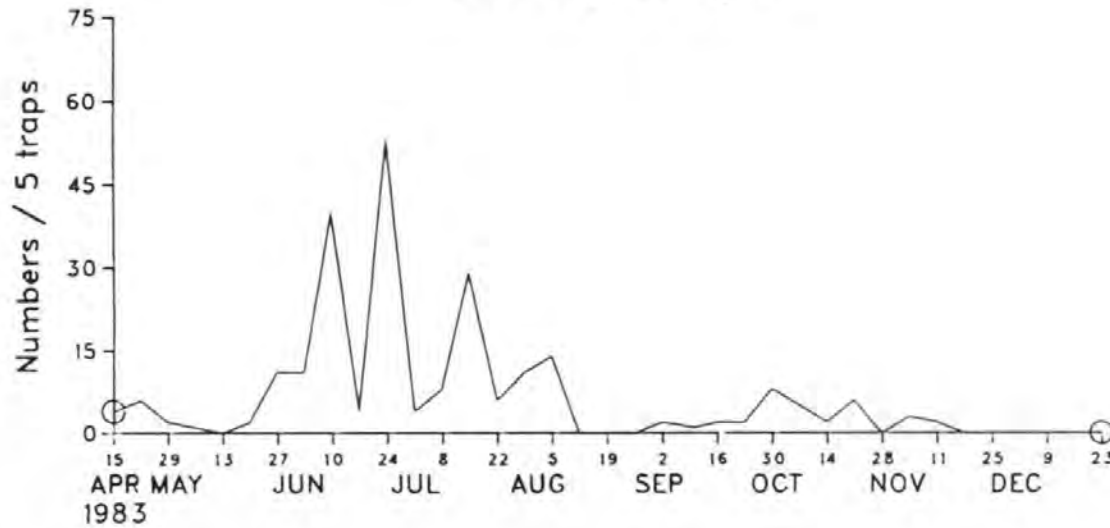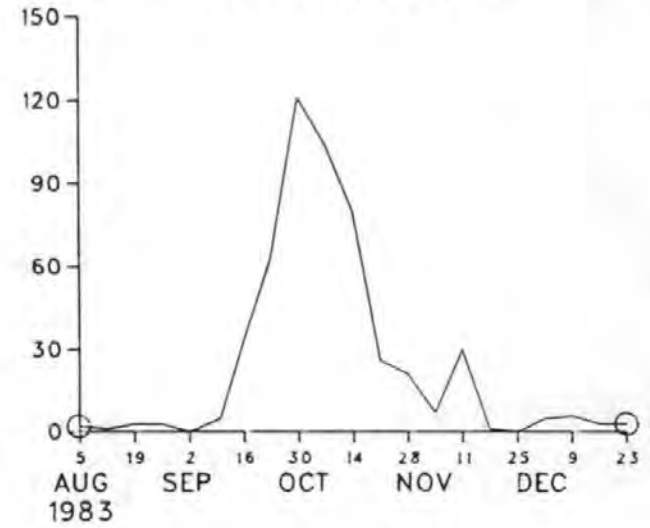
Figure 4.3: Nebria brevicollis, Battisborough Cross 1983
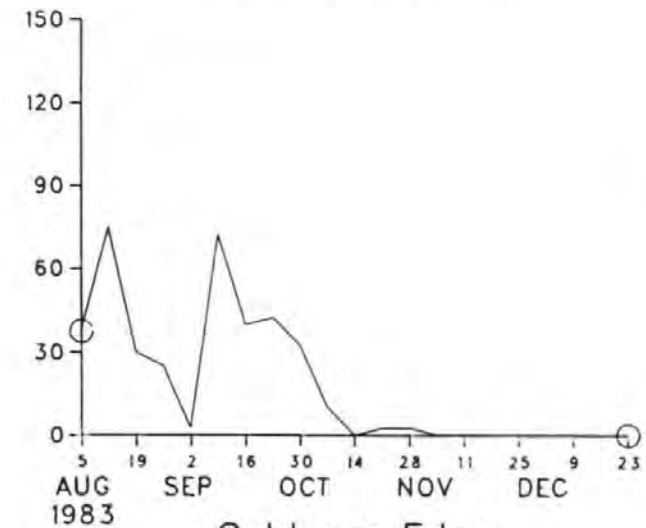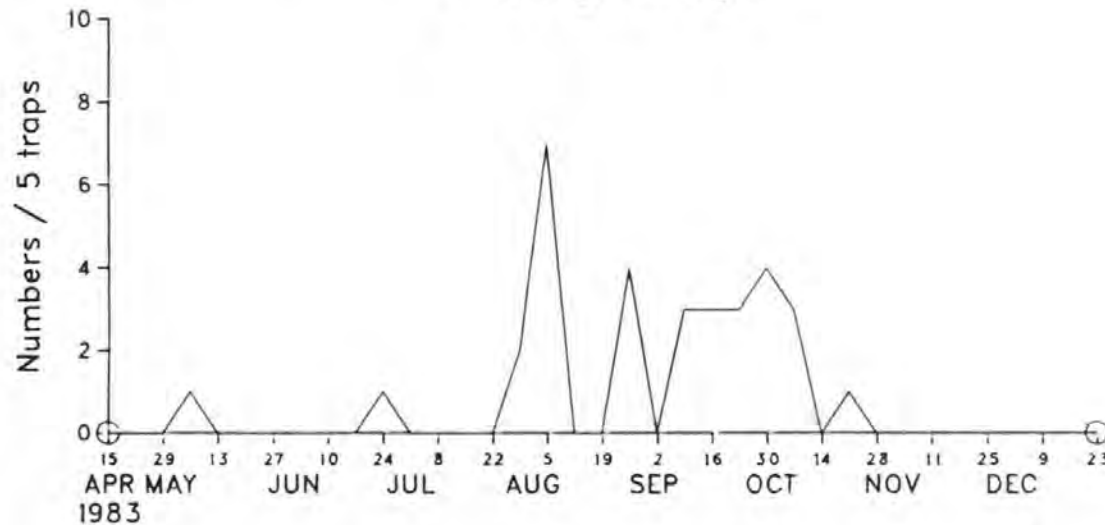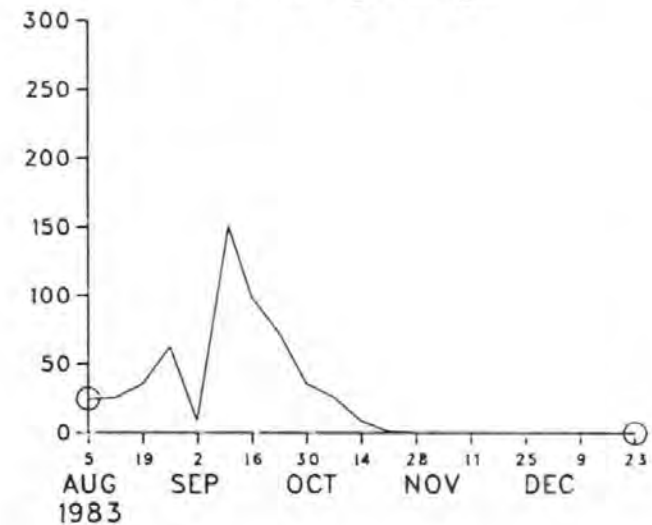
Figure 4.4: Pterostichus melanarius, Battisborough Cross 1983
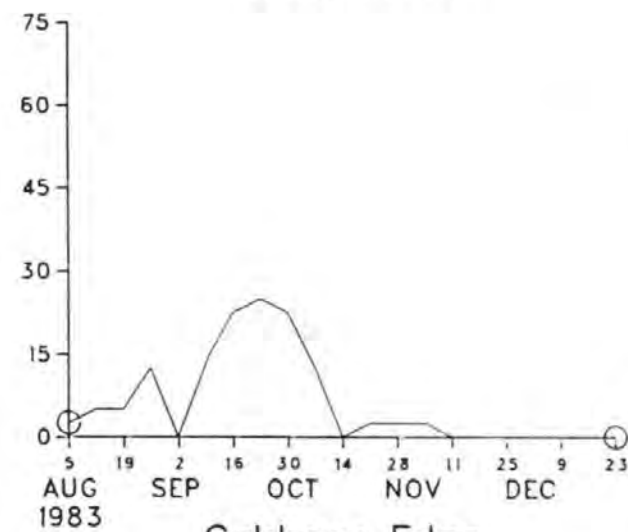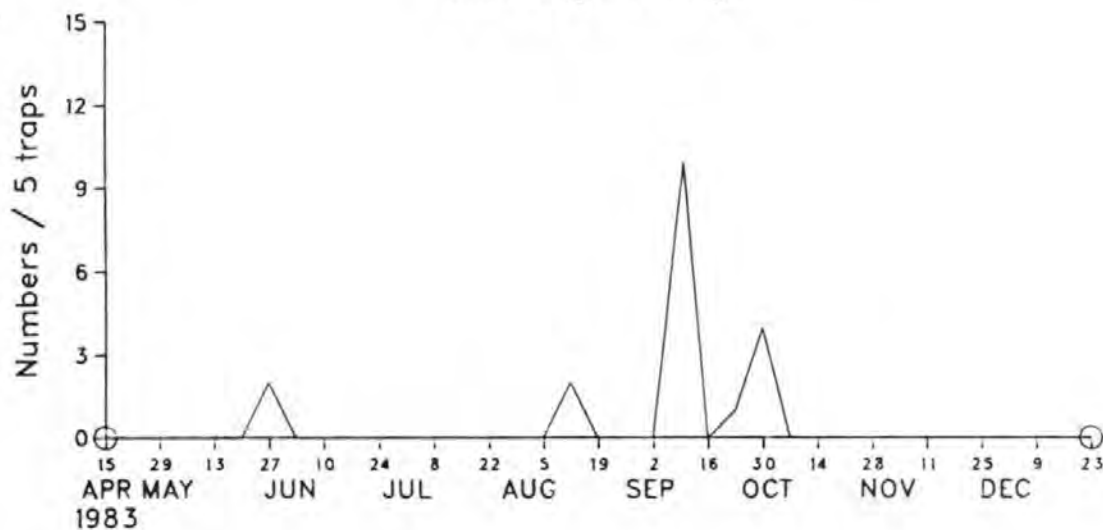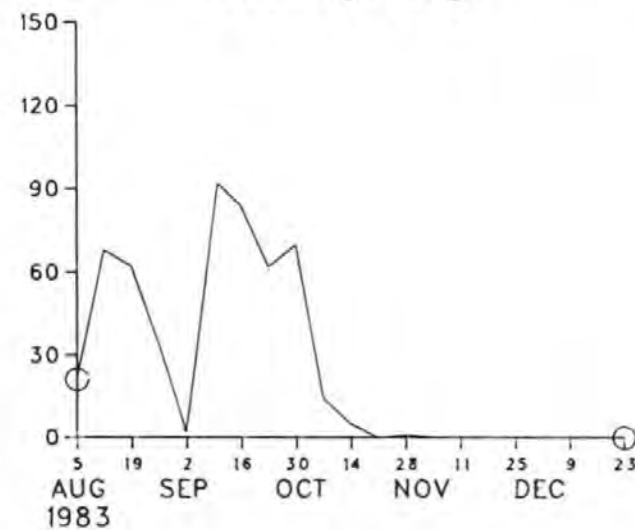
Figure 4.5: Harpalus rufipes, Battisborough Cross 1983

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Weekly minimum temperature

Weekly mean rainfall

Fallow Hedge

Edge Hedge

Cabbage Hedge

Cabbage Edge

Fallow Hedge

Edge Hedge

Cabbage Hedge
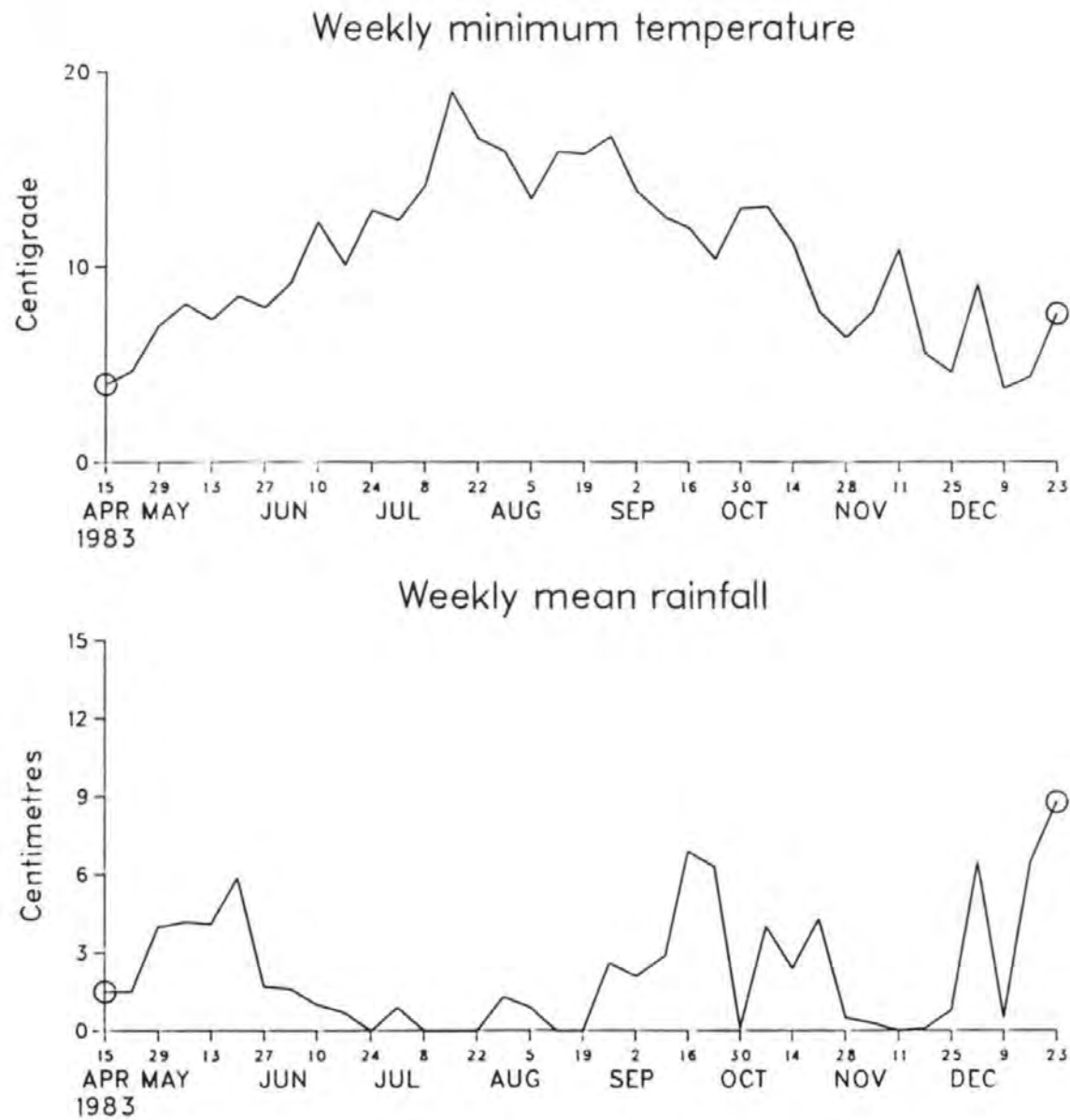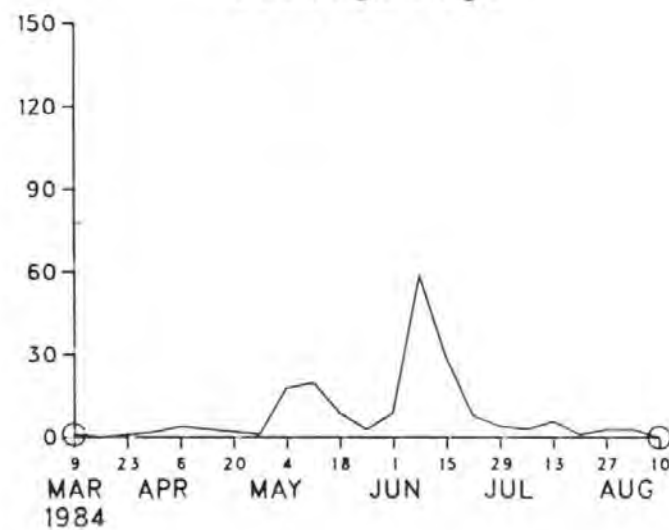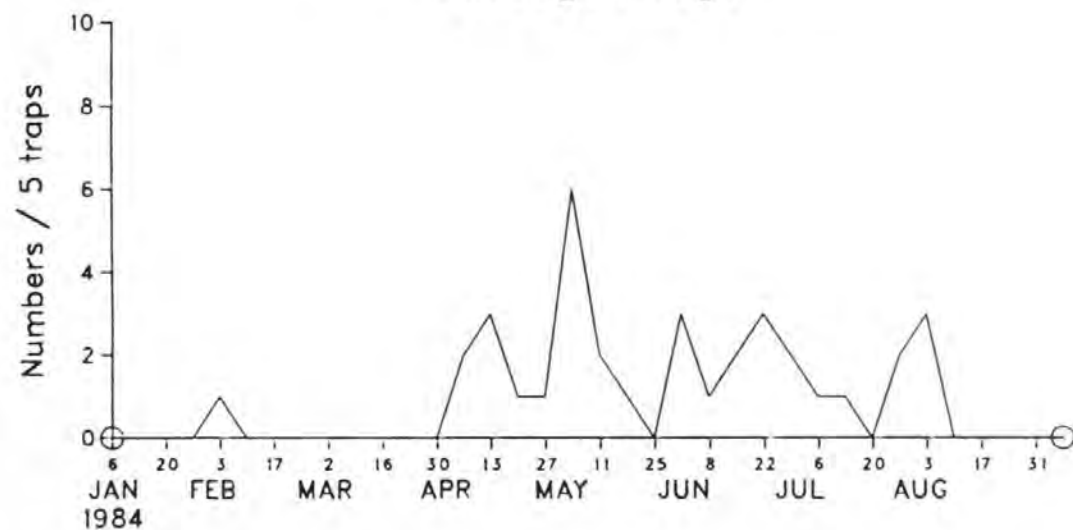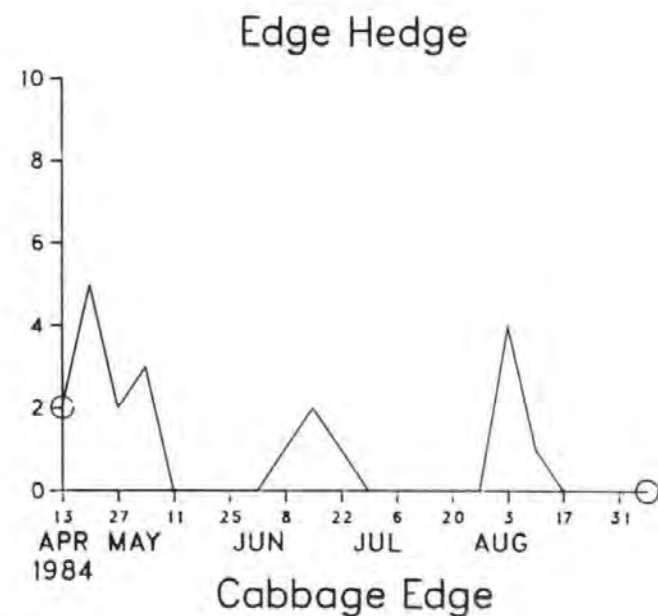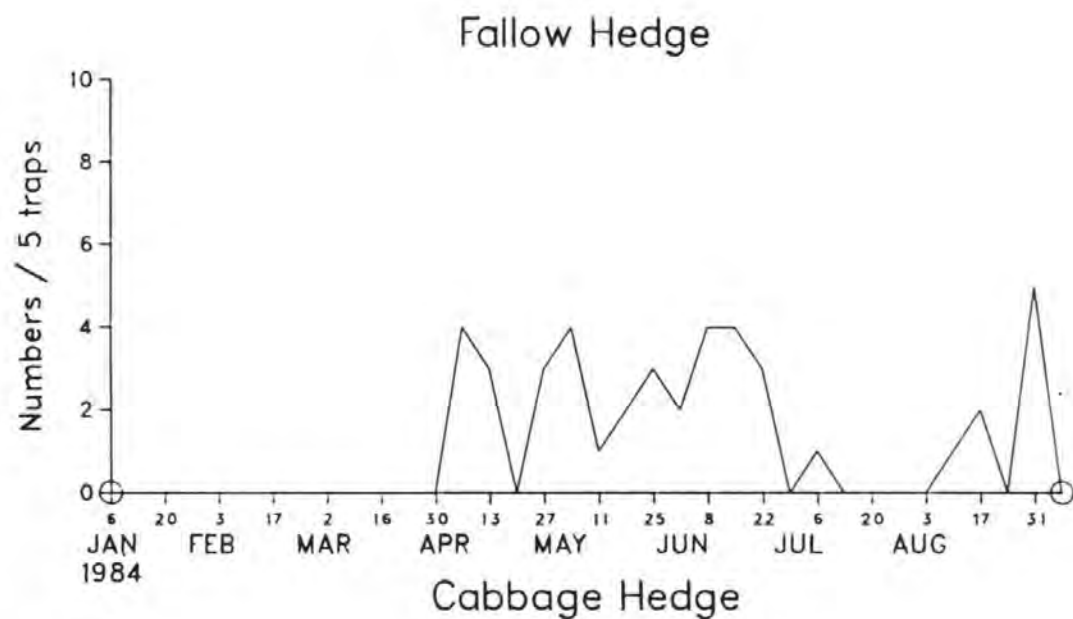
Cabbage Edge

Figure 4.8: Agonum dorsale, Battisborough Cross 1984
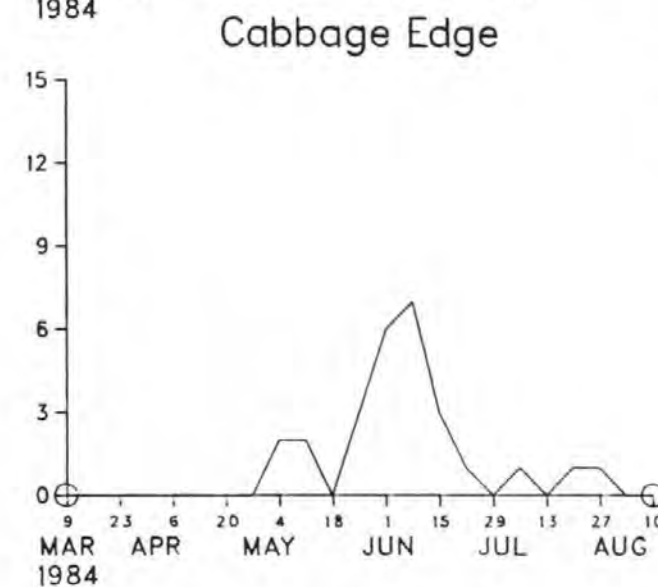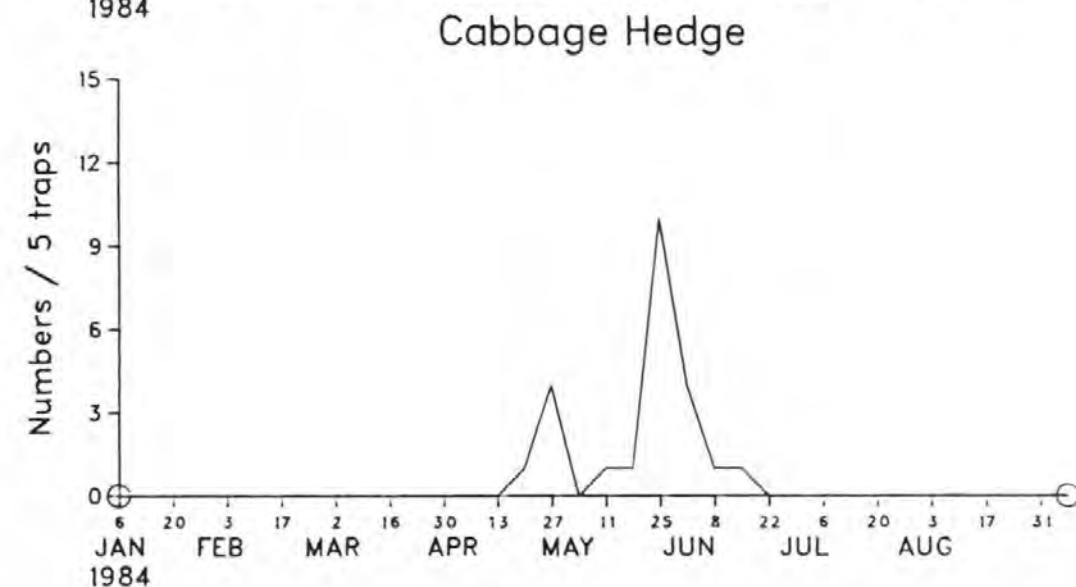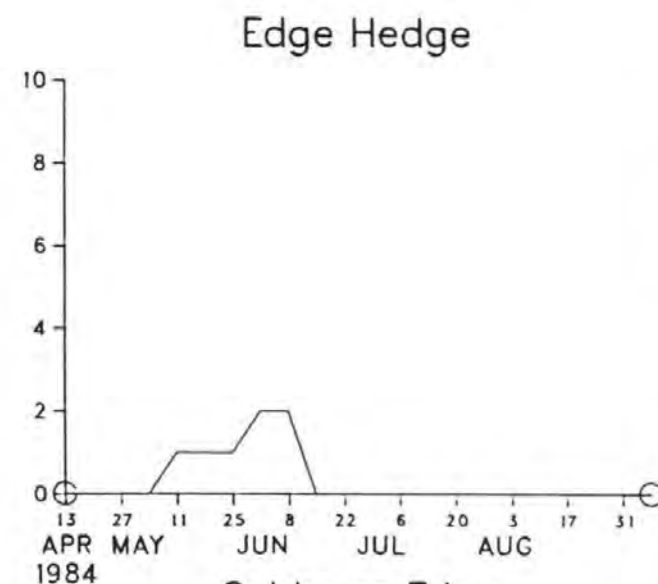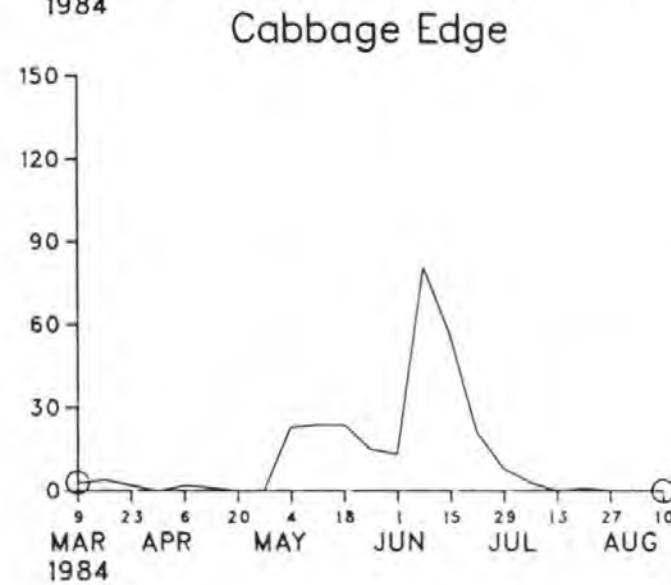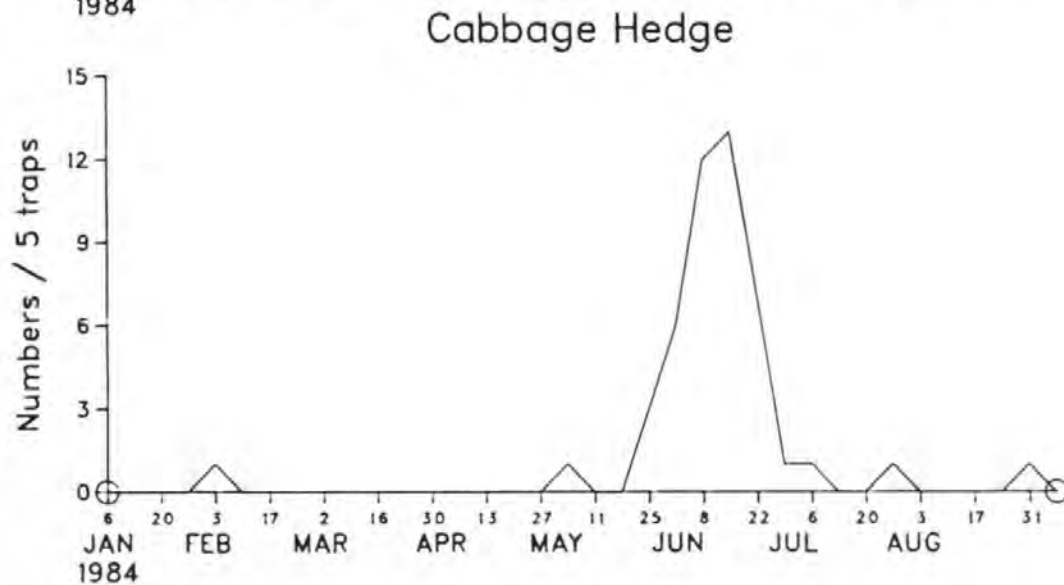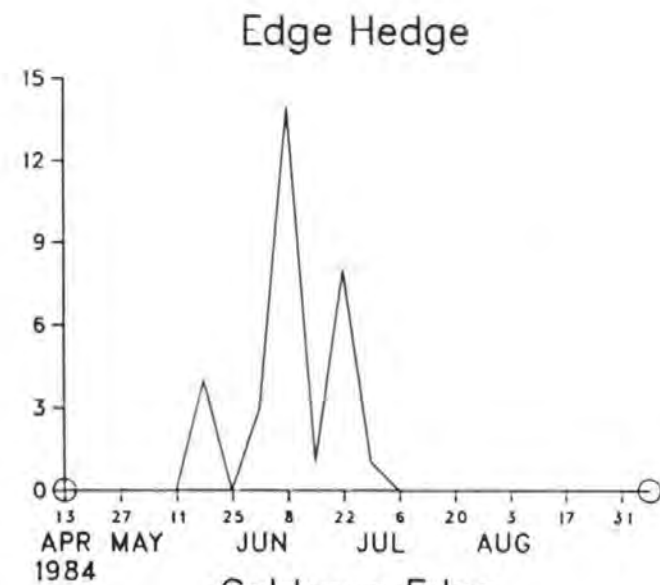
Figure 4.9: Nebria brevicollis, Battisborough Cross 1984

Pterostichus cupreus Cabbage Edge
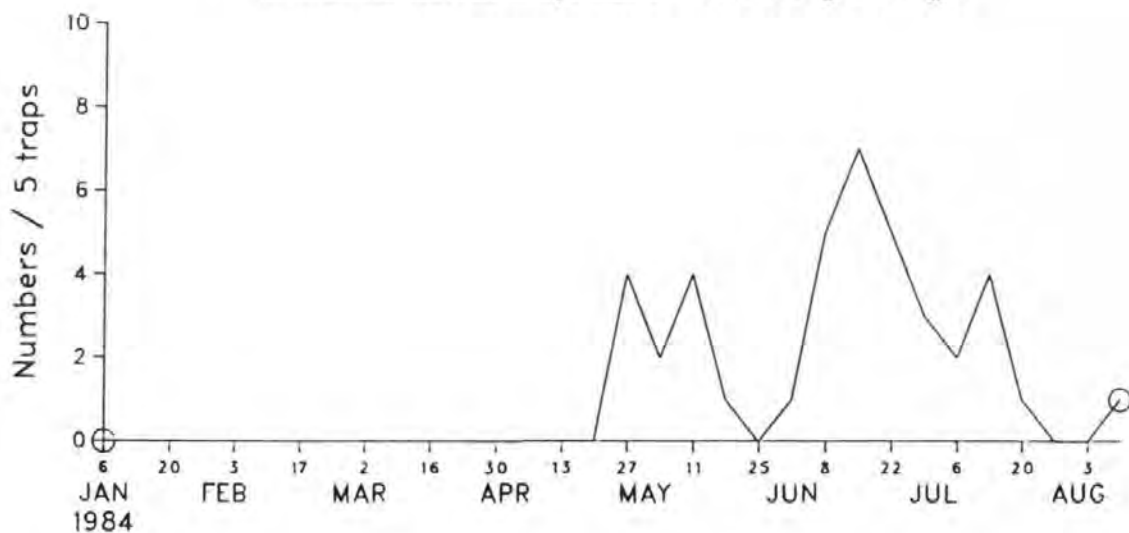
Pterostichus melanarius Cabbage Edge
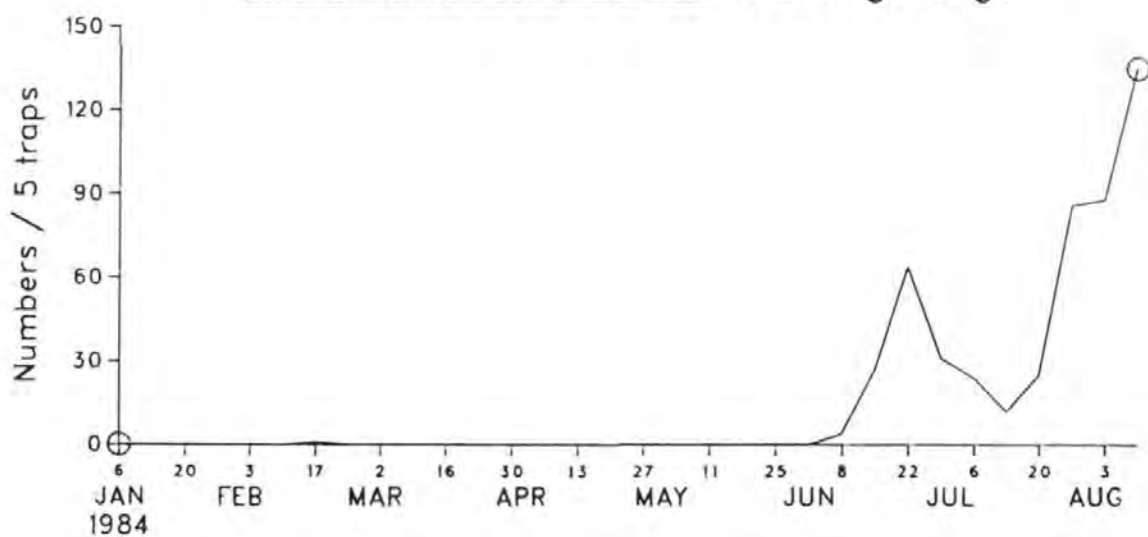
Harpalus rufipes Cabbage Edge

Trechus quadristriatus Cabbage Hedge

Amara ovata Edge Hedge

Amara ovata Cabbage Edge

Amara aenea Cabbage Edge

Amara plebeja Cabbage Edge

Agonum muelleri Cabbage Edge

Weekly minimum temperature

Weekly mean rainfall

Weekly mean humidity
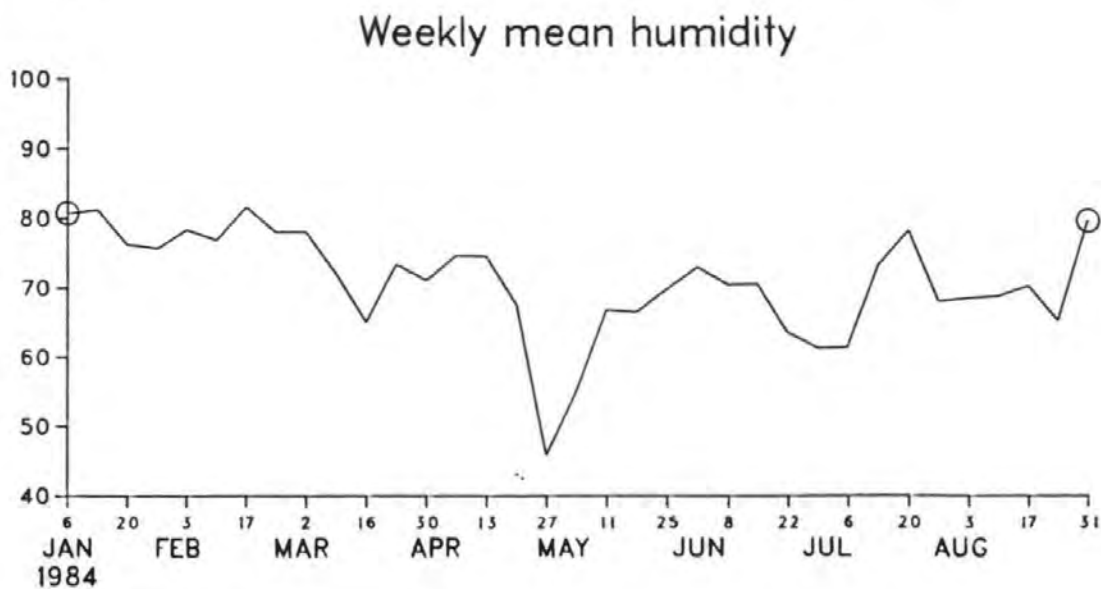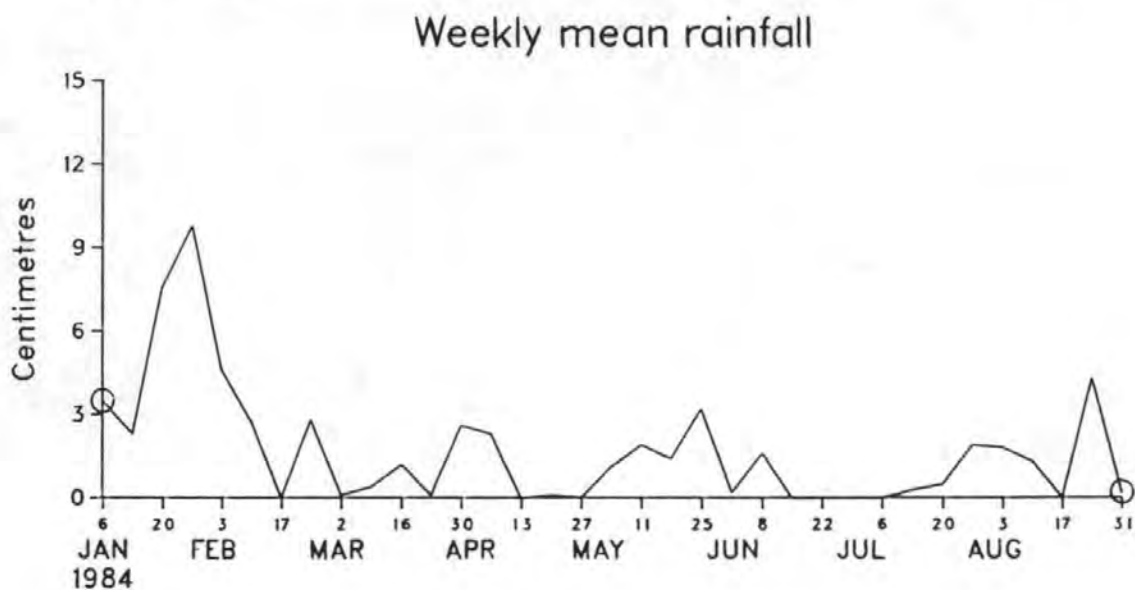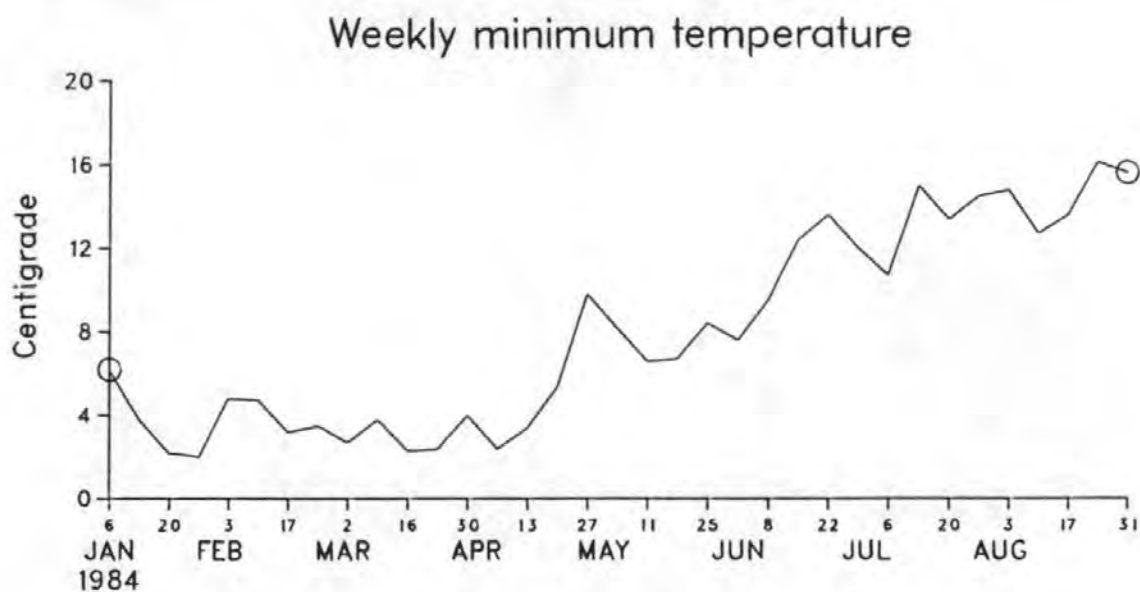
Figure 4.14: Staddon Heights 1984

Pterostichus melanarius

Nebria brevicollis
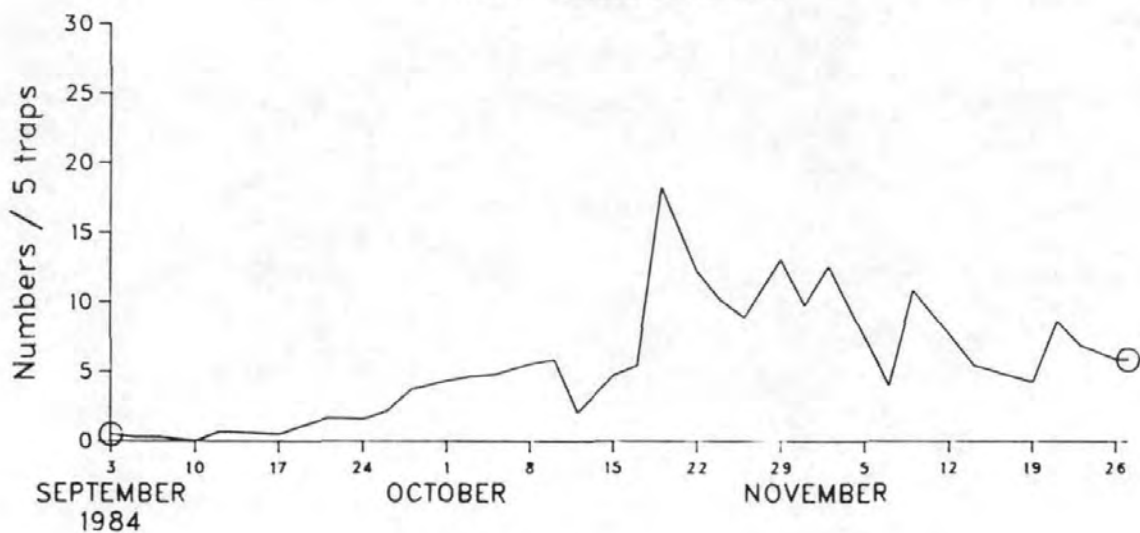
Trechus quadristriatus

Mean minimum temperature

Mean total rainfall

Mean humidity
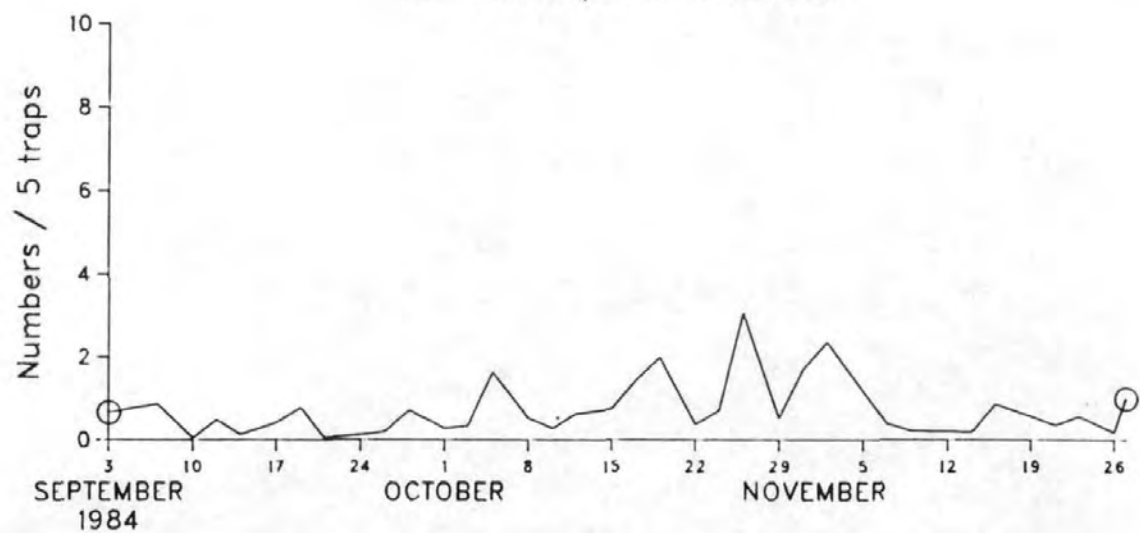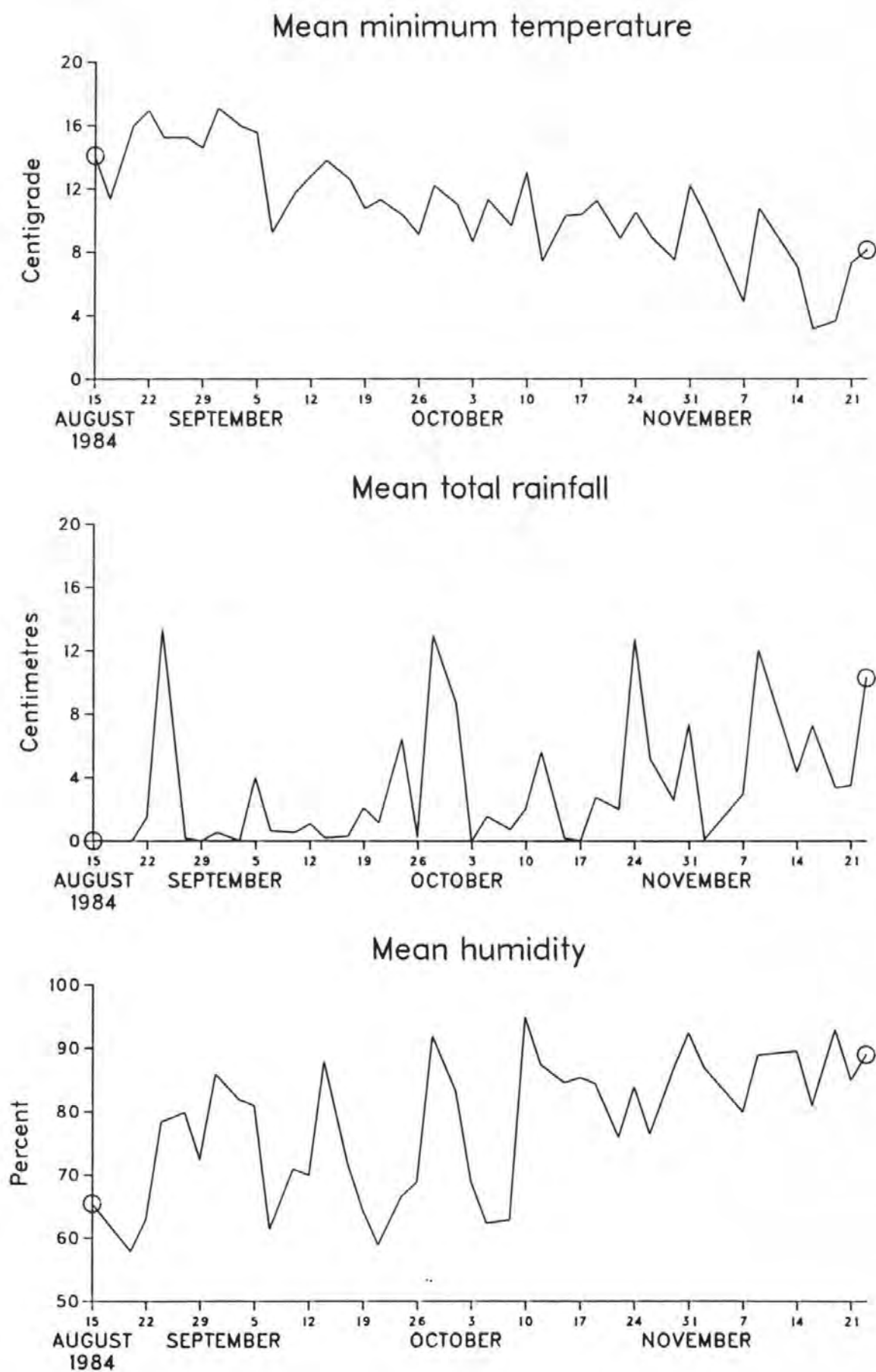
Pterostichus cupreus Pitfalls
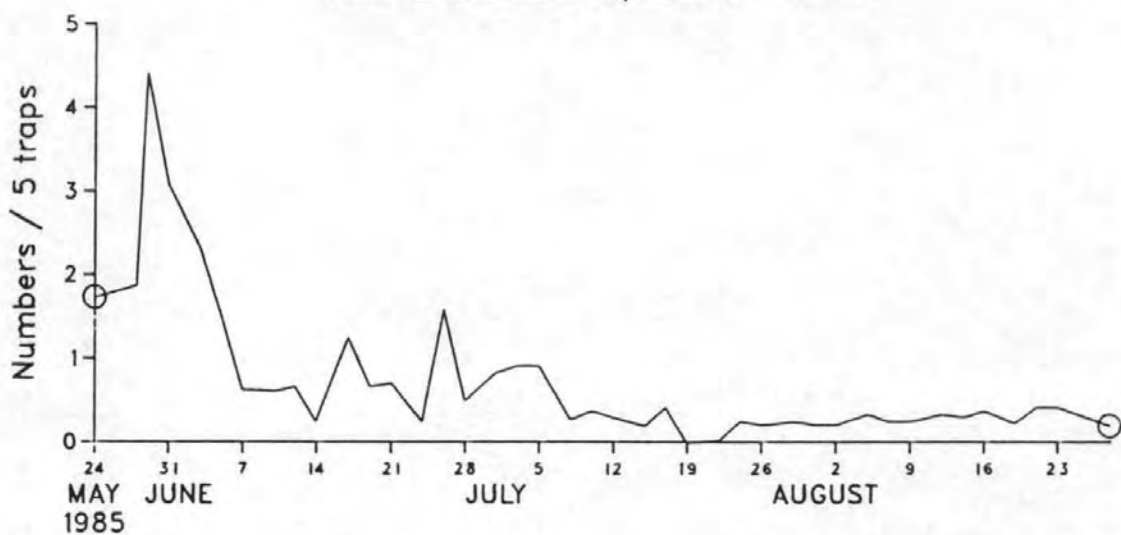
Pterostichus cupreus Gutters
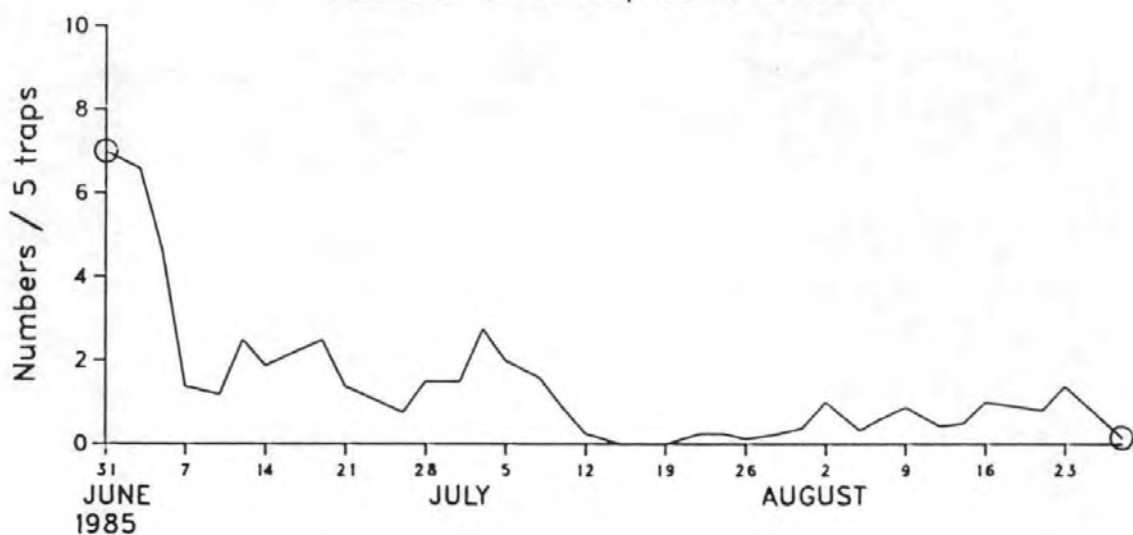
Trechus quadristriatus Pitfalls
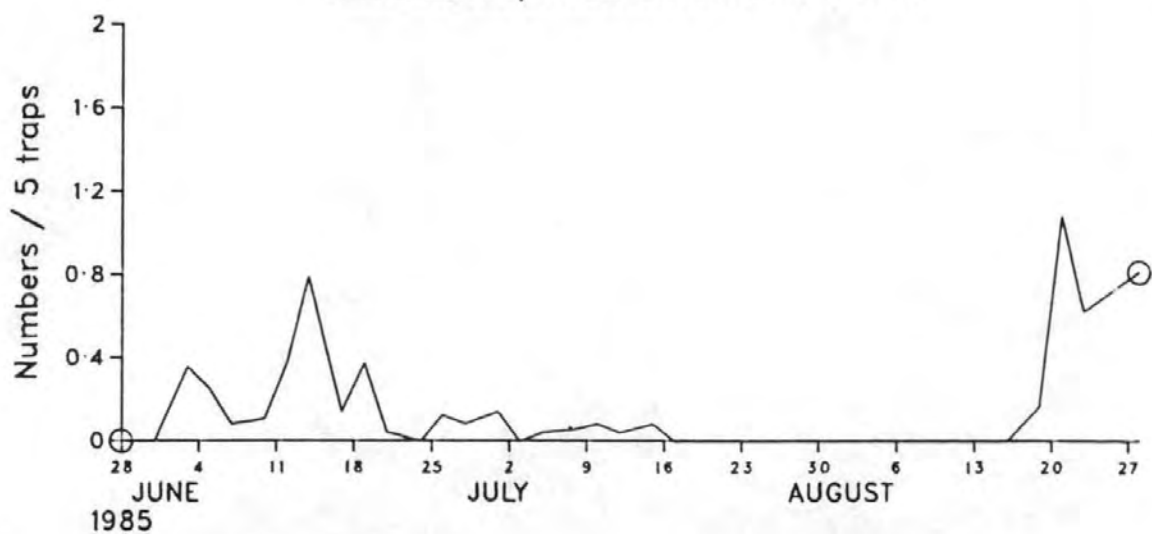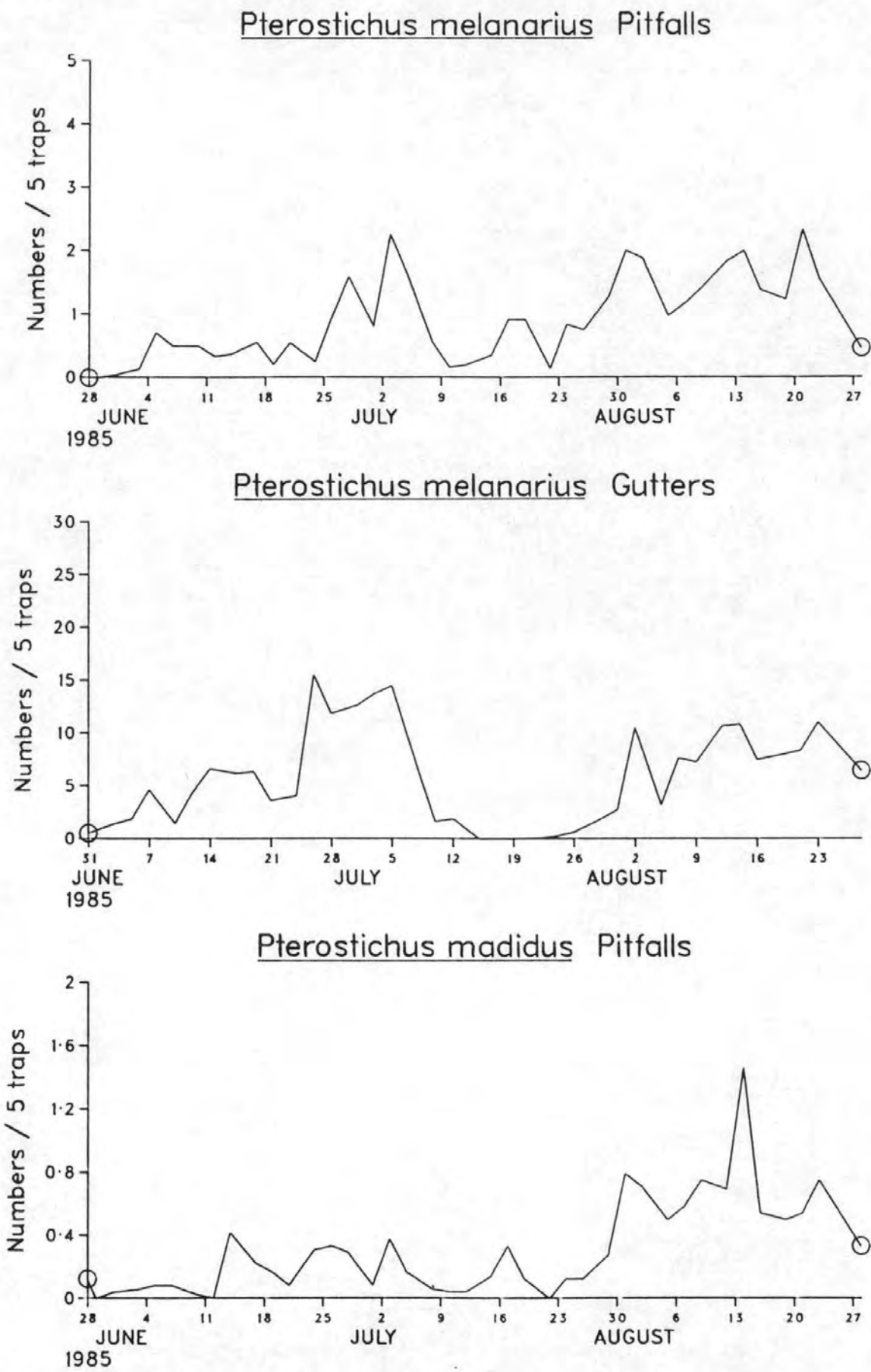
Pterostichus melanarius Pitfalls

Pterostichus melanarius Gutters

Pterostichus madidus Pitfalls

Harpalus rufipes Pitfalls

Harpalus rufipes Gutters

Pterostichus madidus Gutters

Minimum temperature

Maximum temperature

Mean total rainfall

Mean humidity

Mean rainfall AM

Mean rainfall PM

Nebria brevicollis Pitfalls

Nebria brevicollis North Gutters

Nebria brevicollis West Gutters

Pterostichus melanarius Pitfalls

Pterostichus melanarius North Gutters

Pterostichus melanarius West Gutters

Trechus quadristriatus Pitfalls

Trechus quadristriatus North Gutters

Harpalus rufipes West Gutters
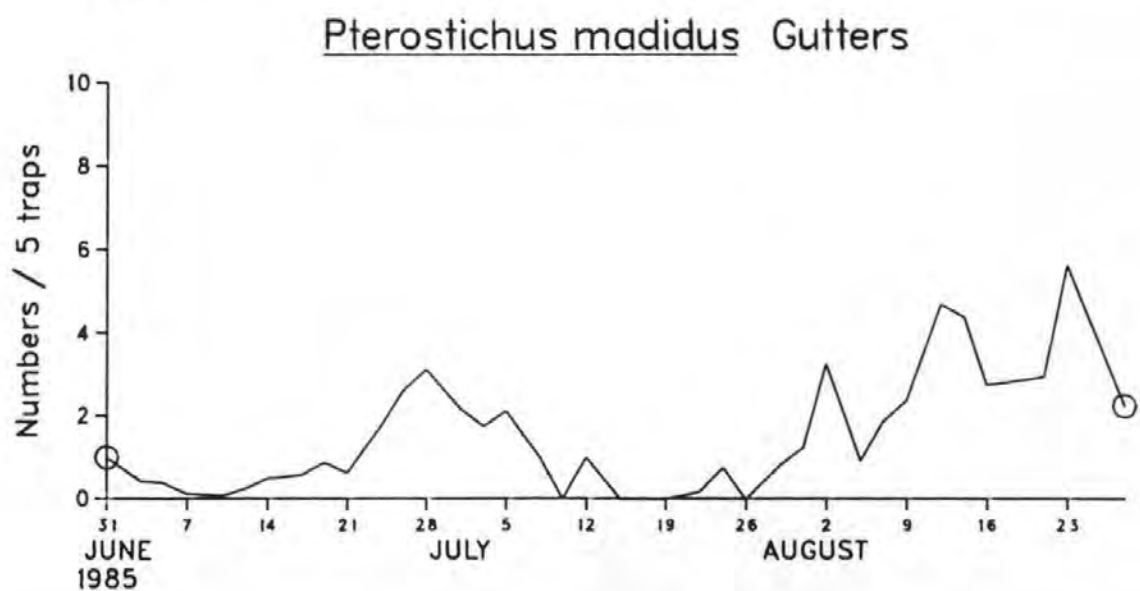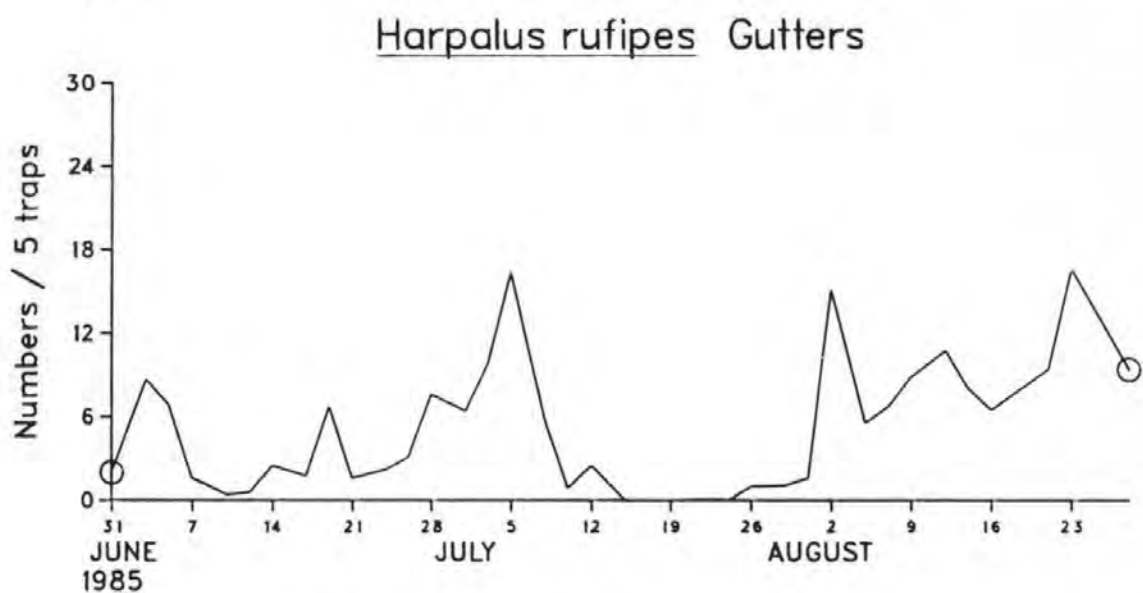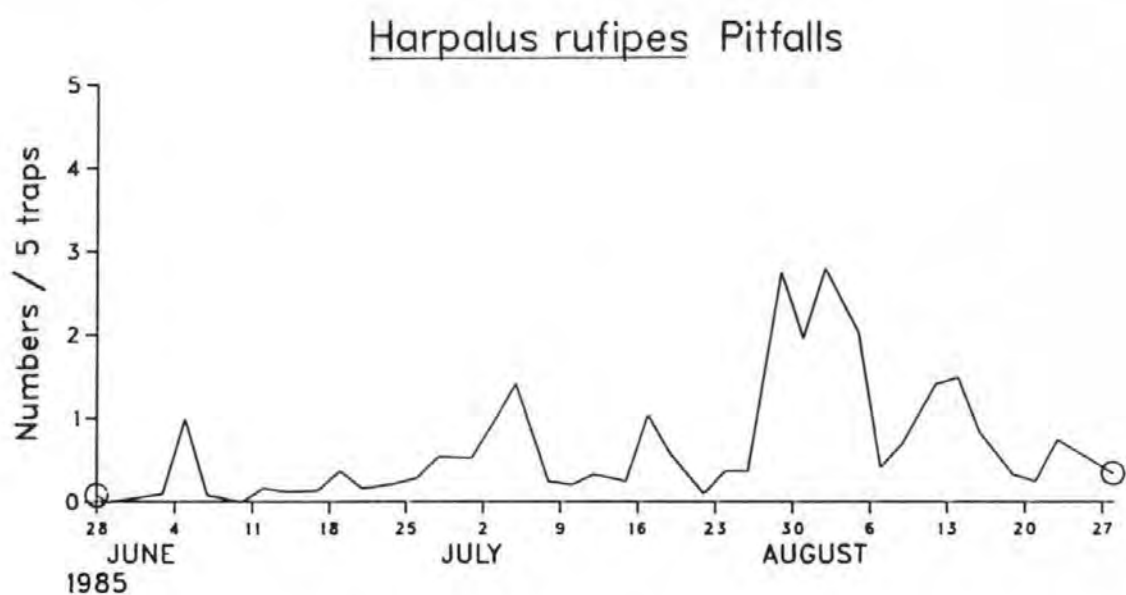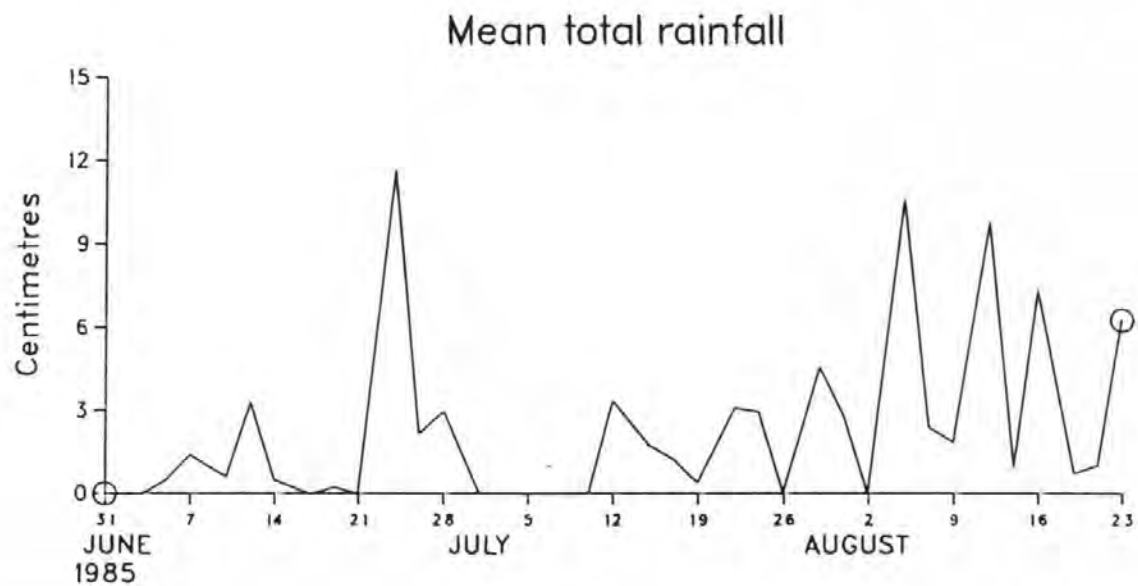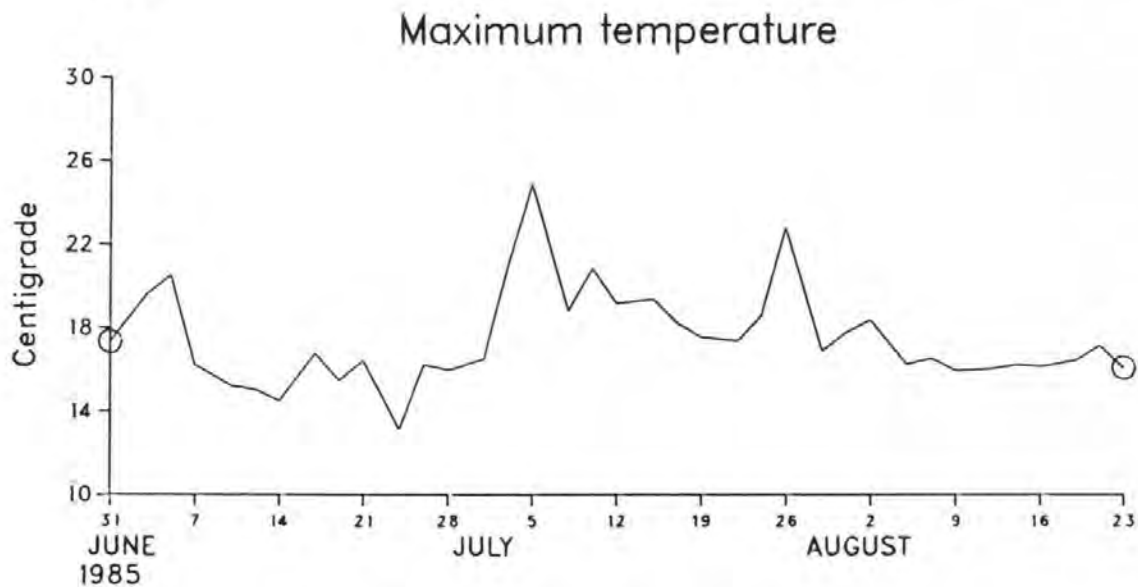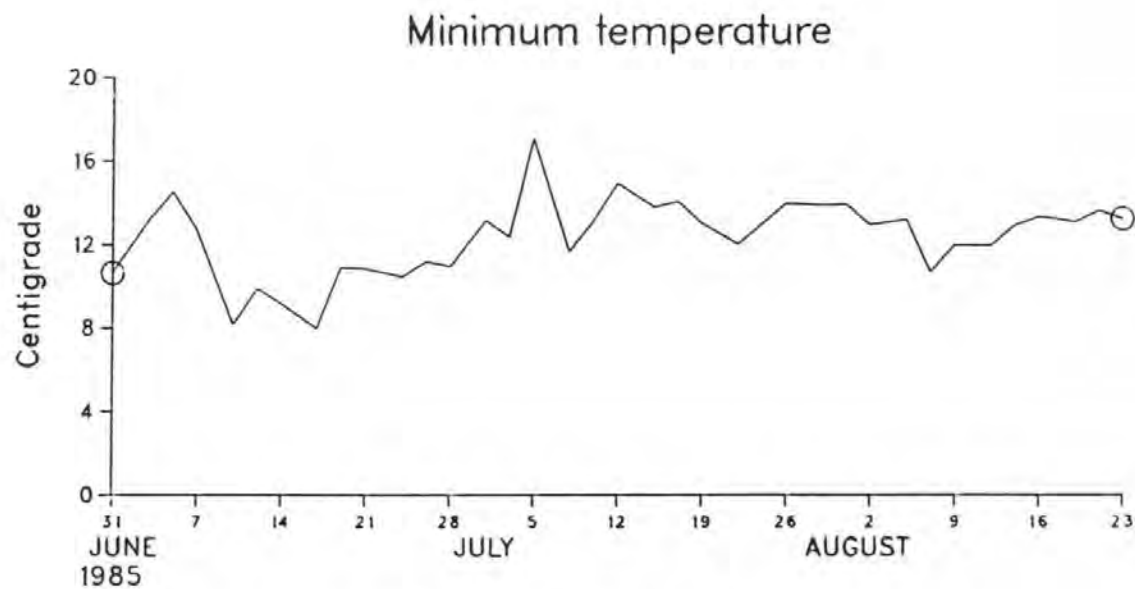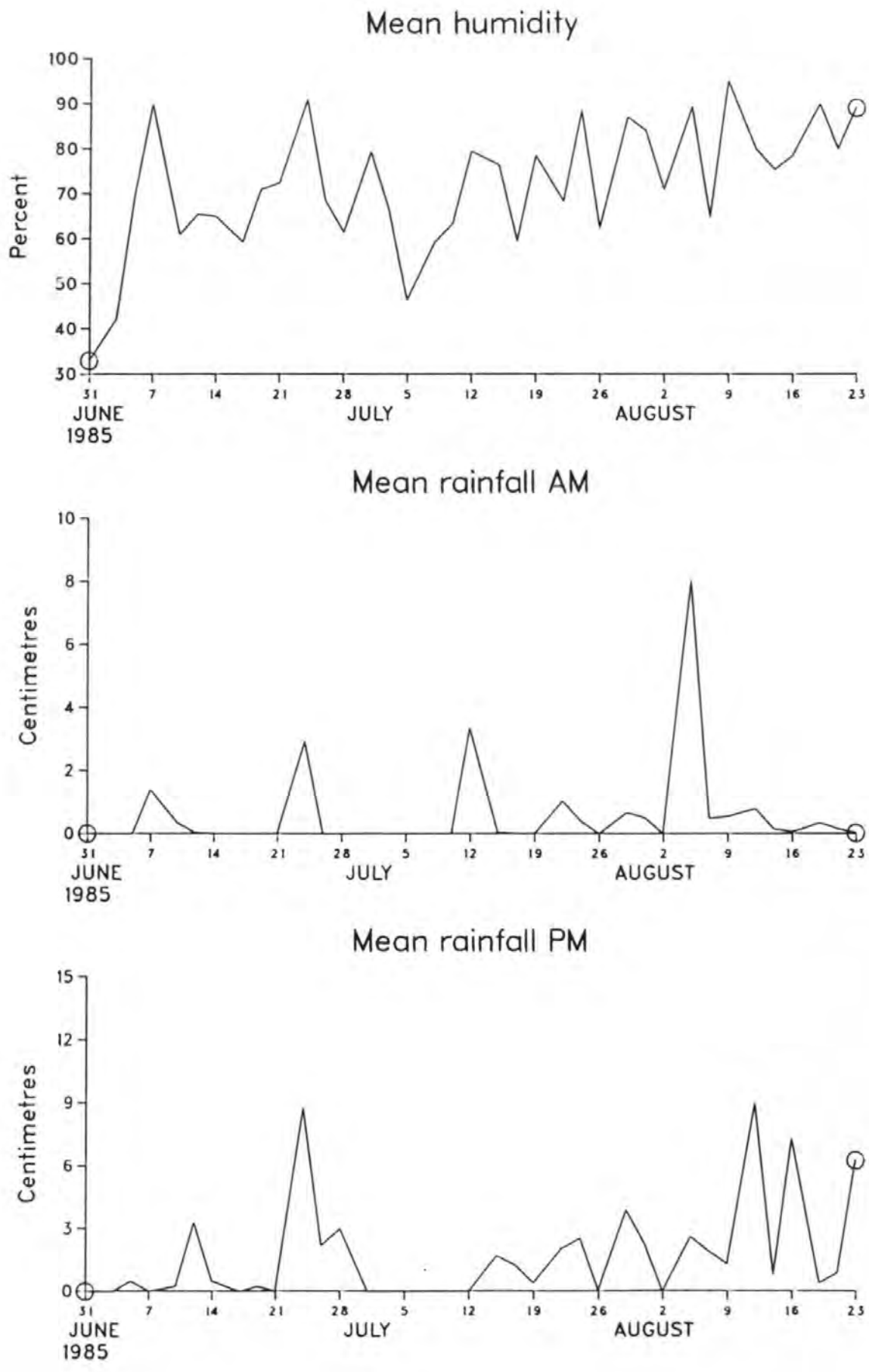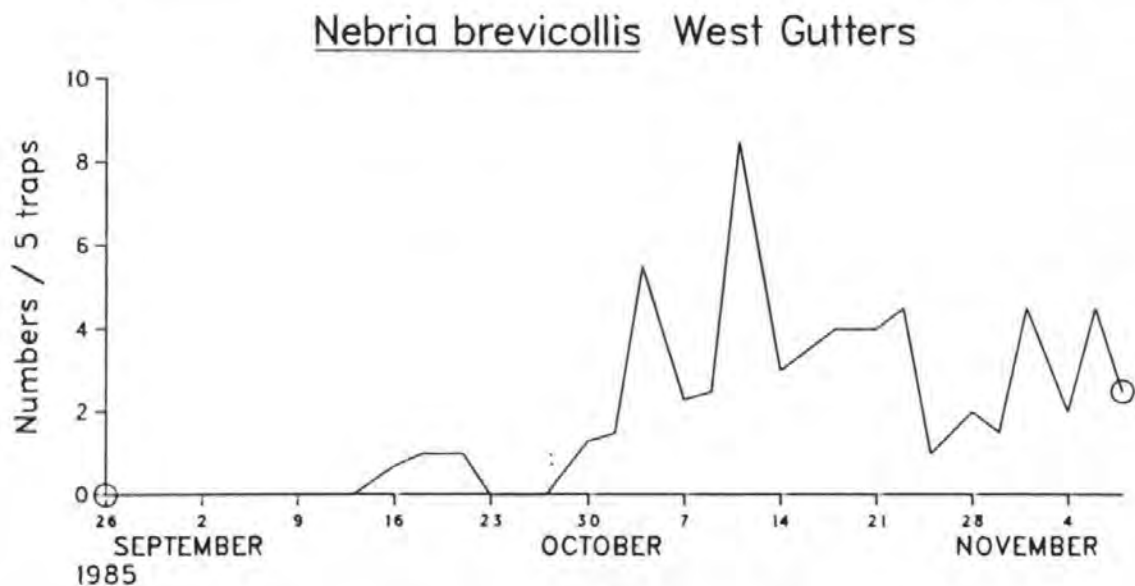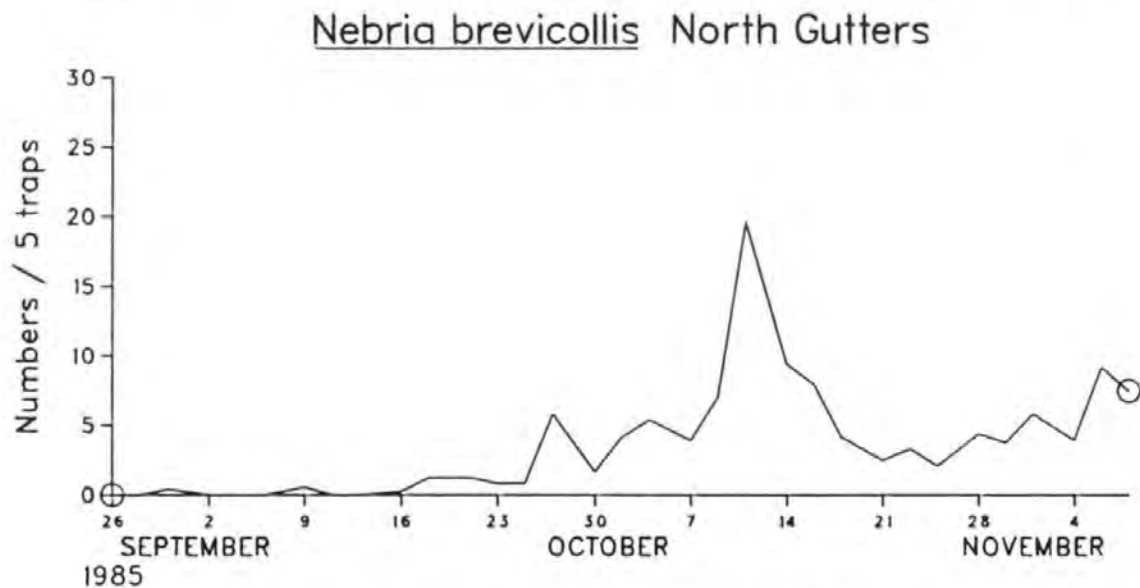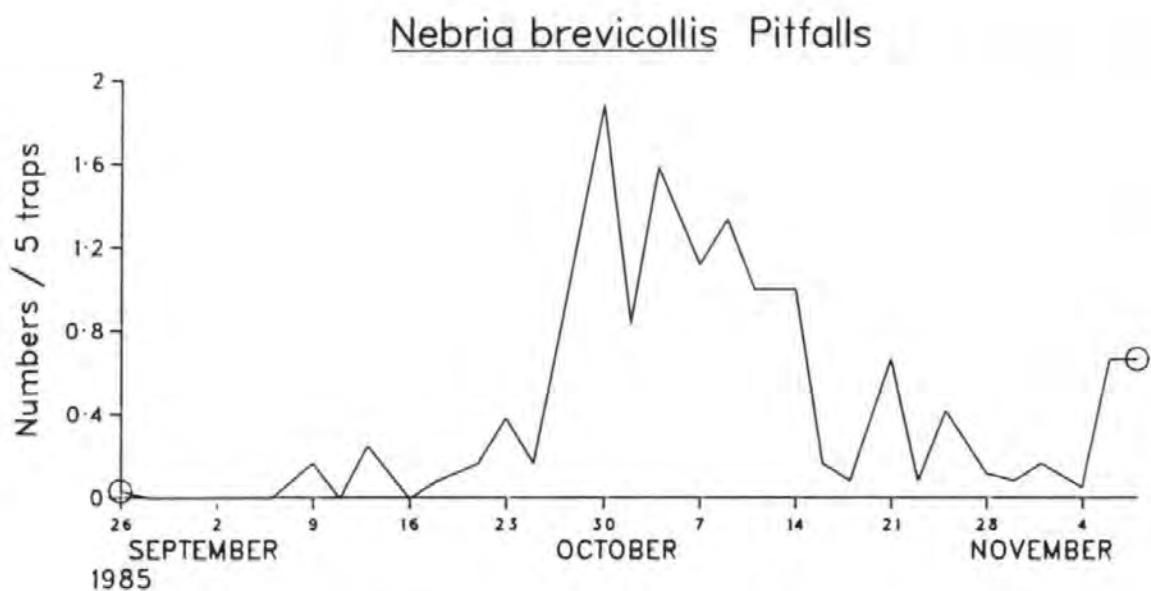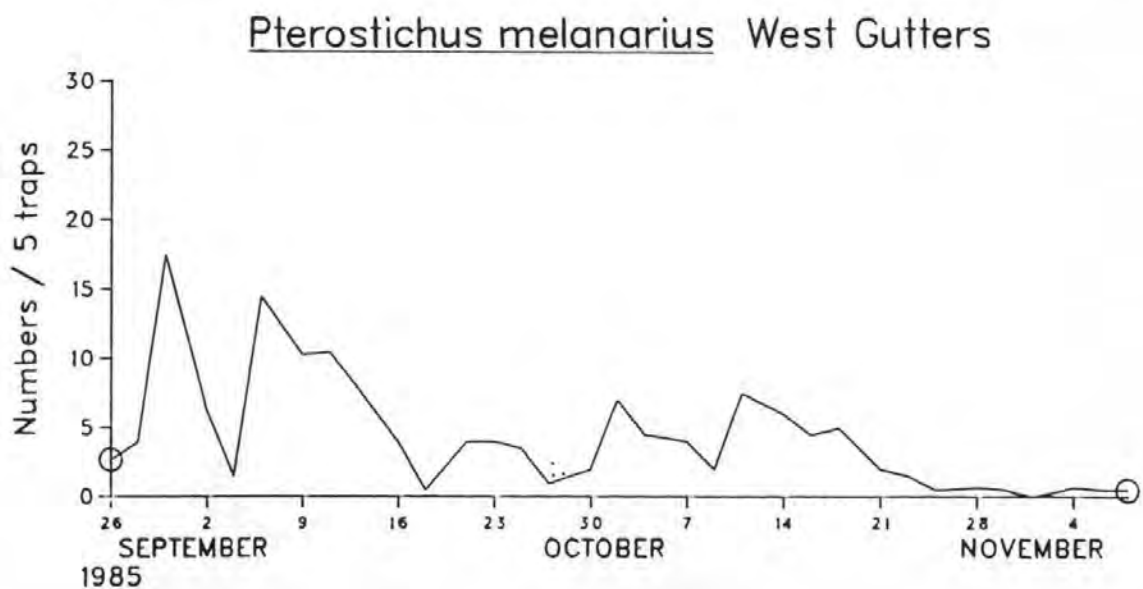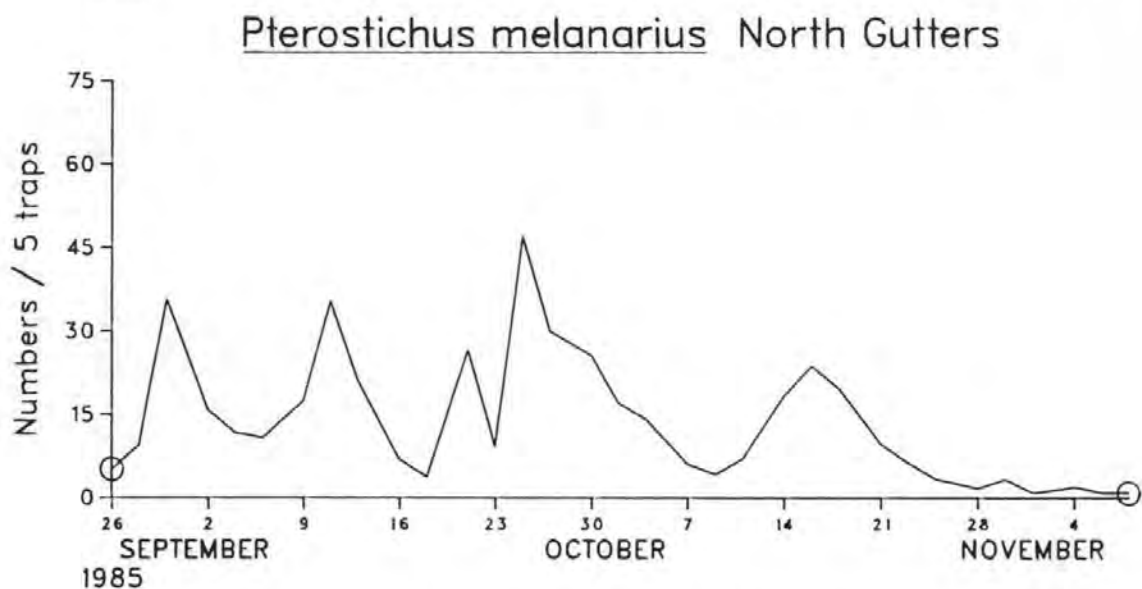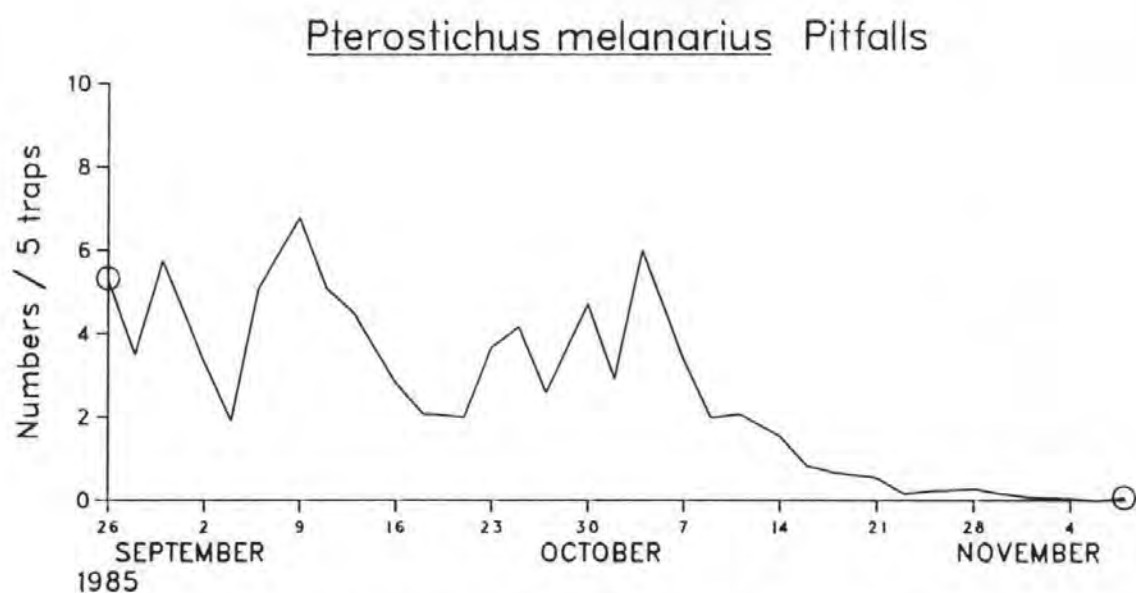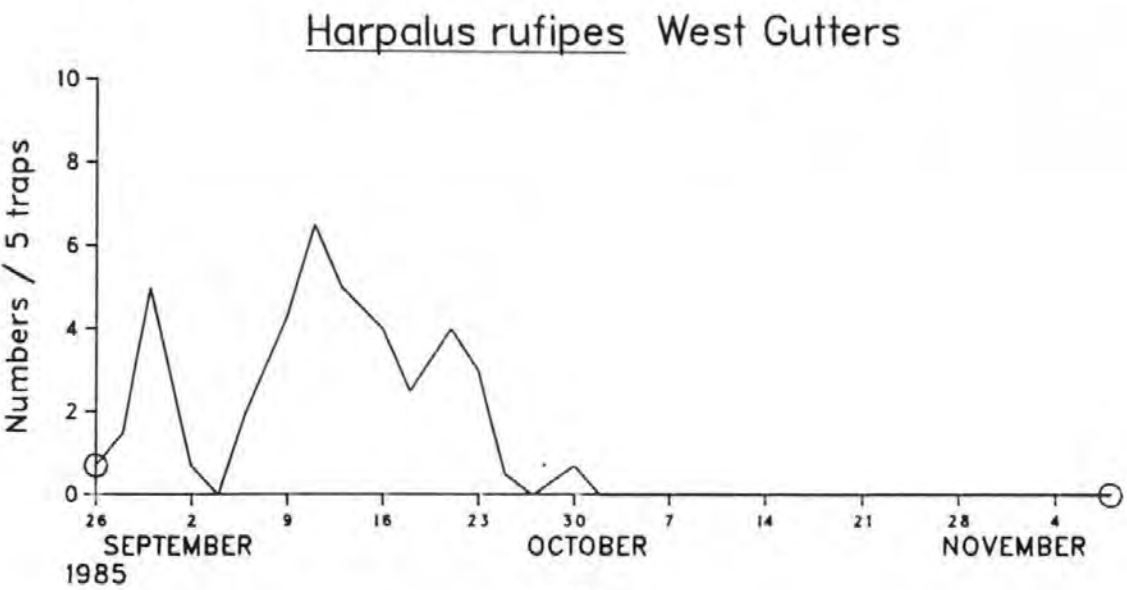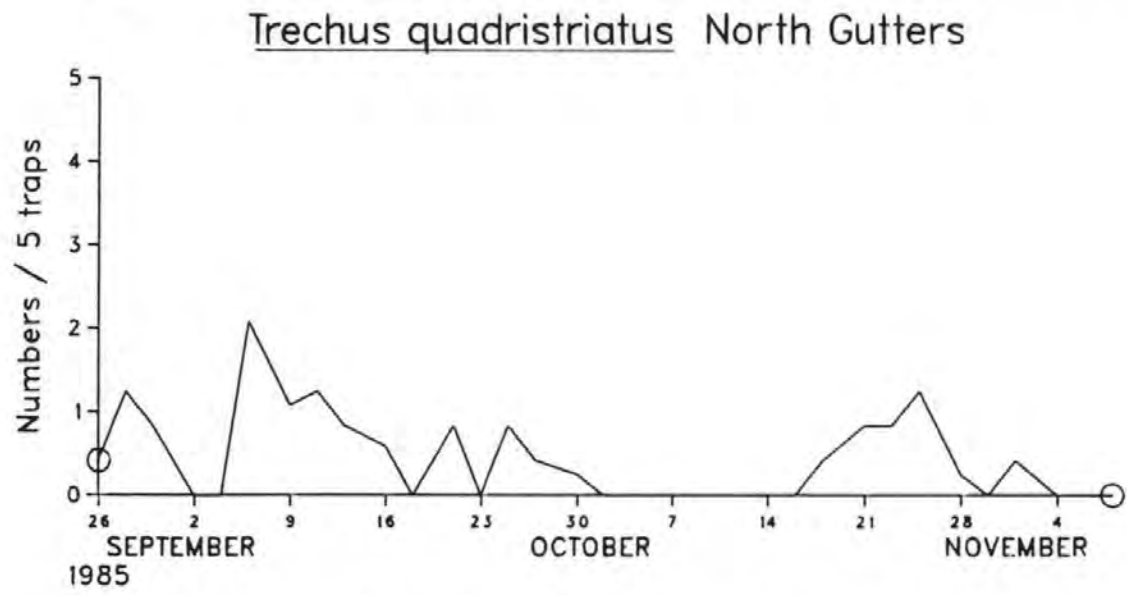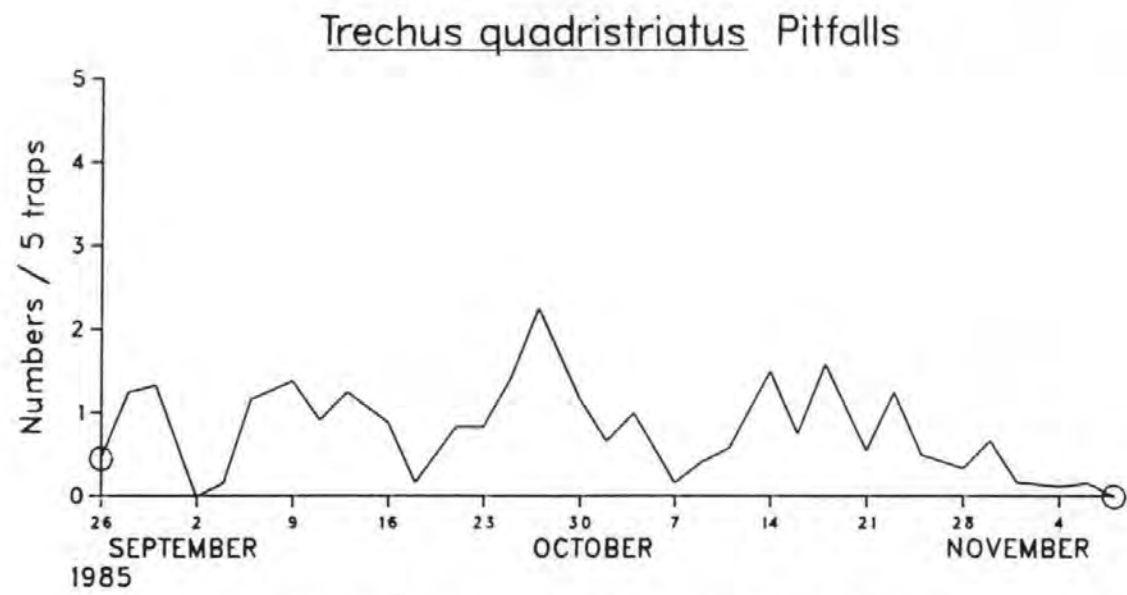
Calathus fuscipes Pitfalls
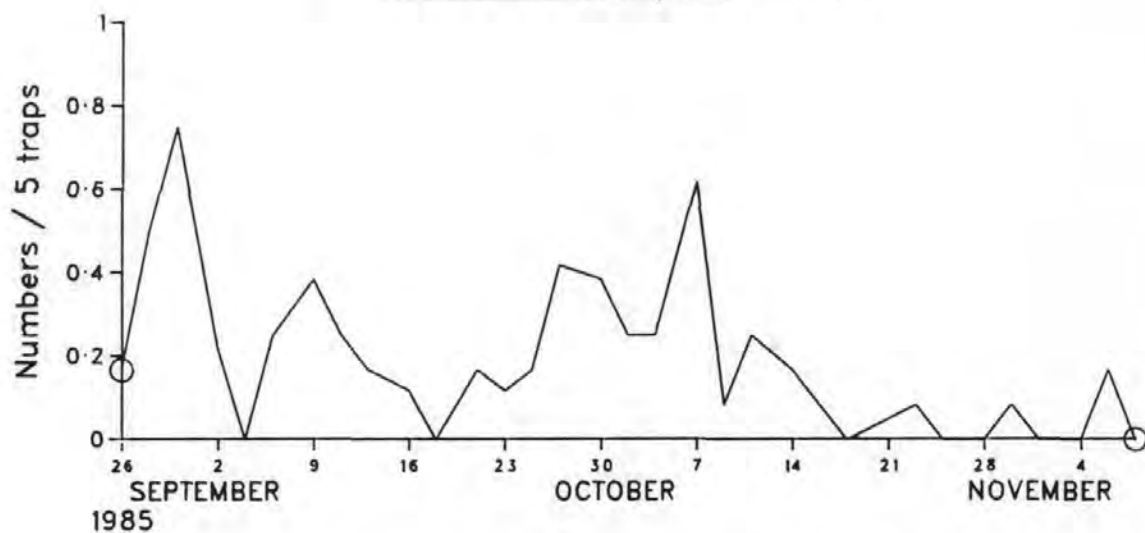
Calathus fuscipes North Gutters
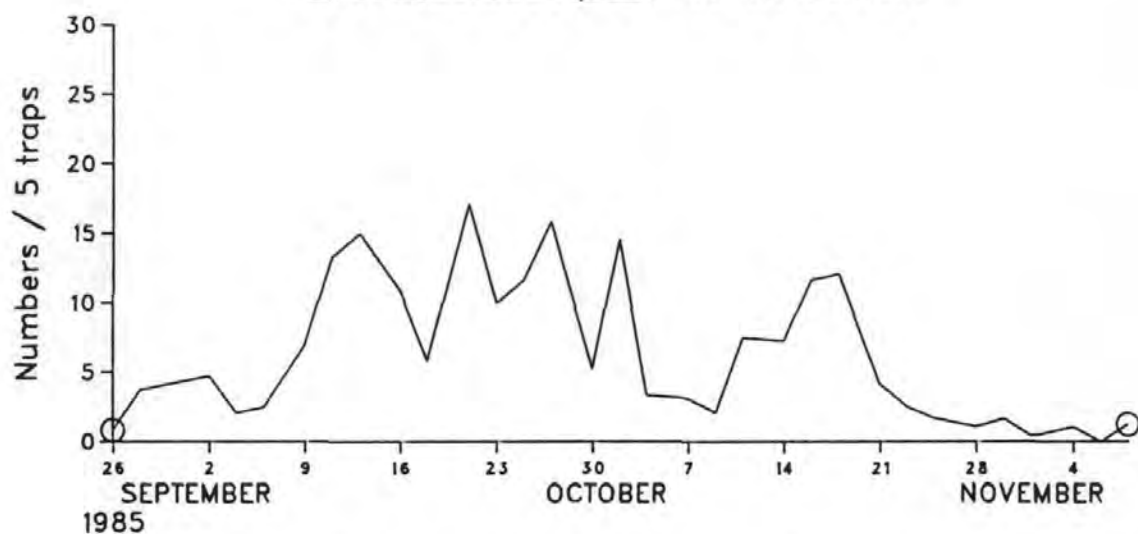
Calathus fuscipes West Gutters

Amara aenea Pitfalls

Amara aenea North Gutters

Amara aenea West Gutters
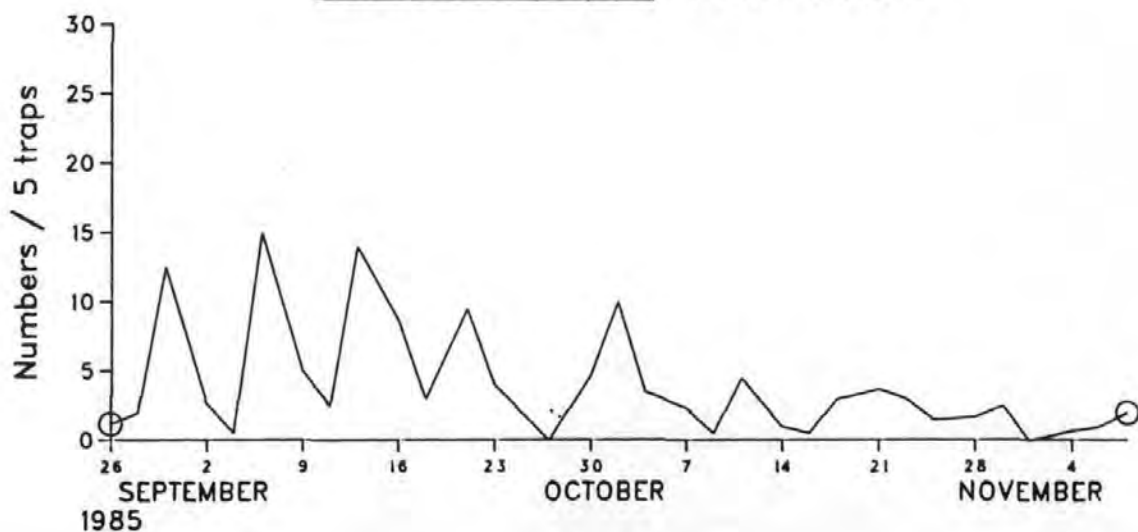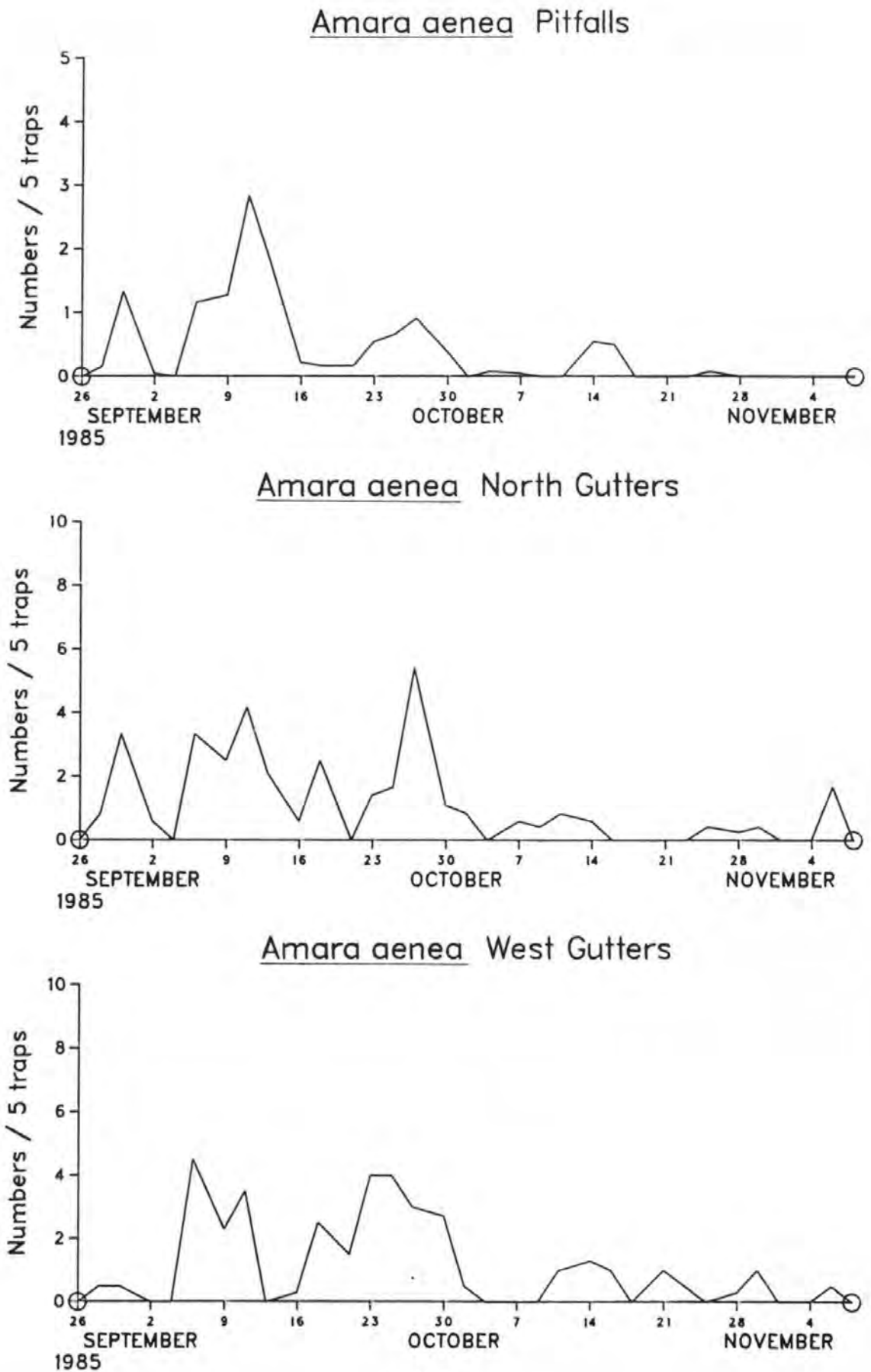
Figure 4.26: Staddon Heights 1985
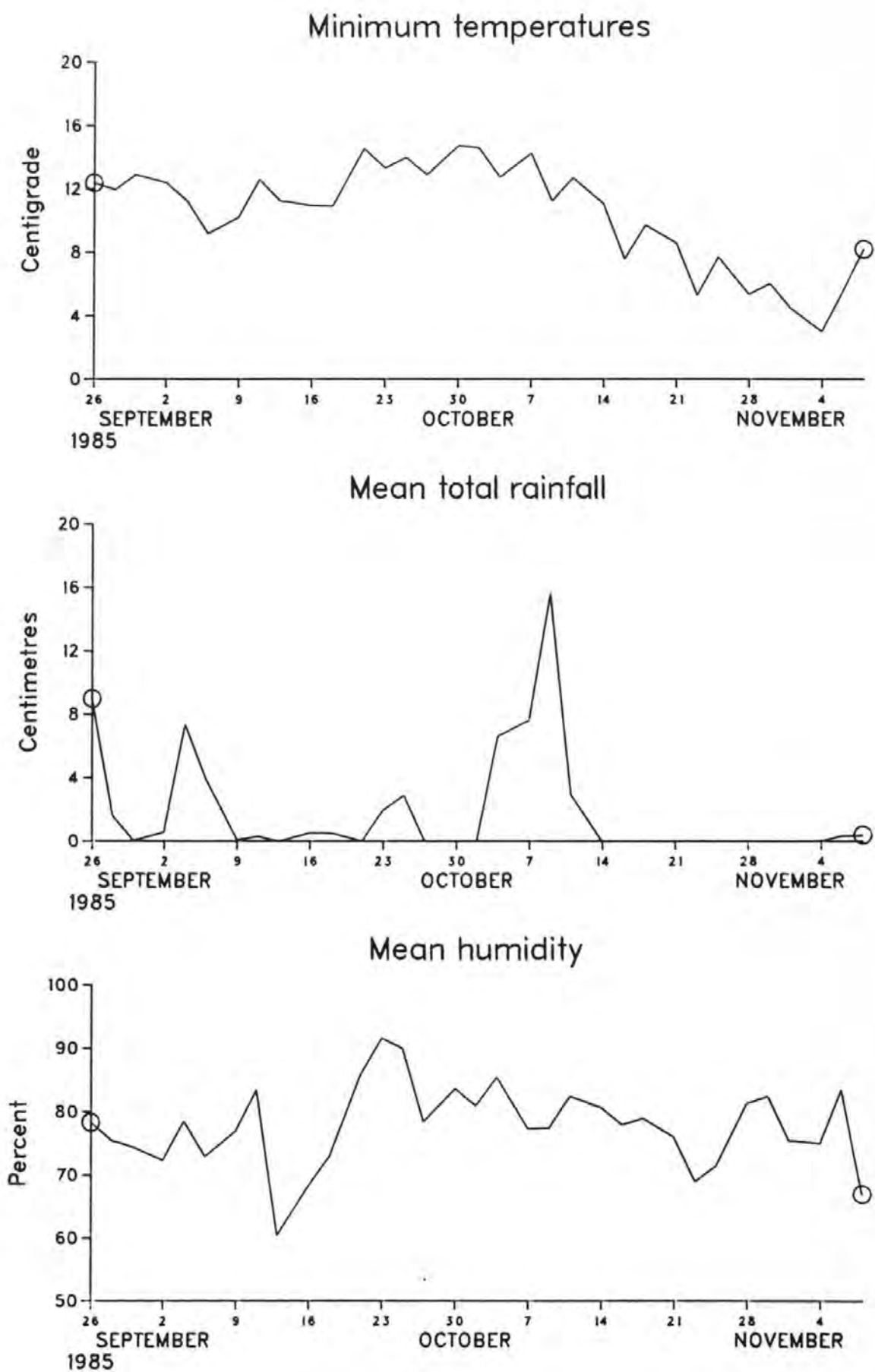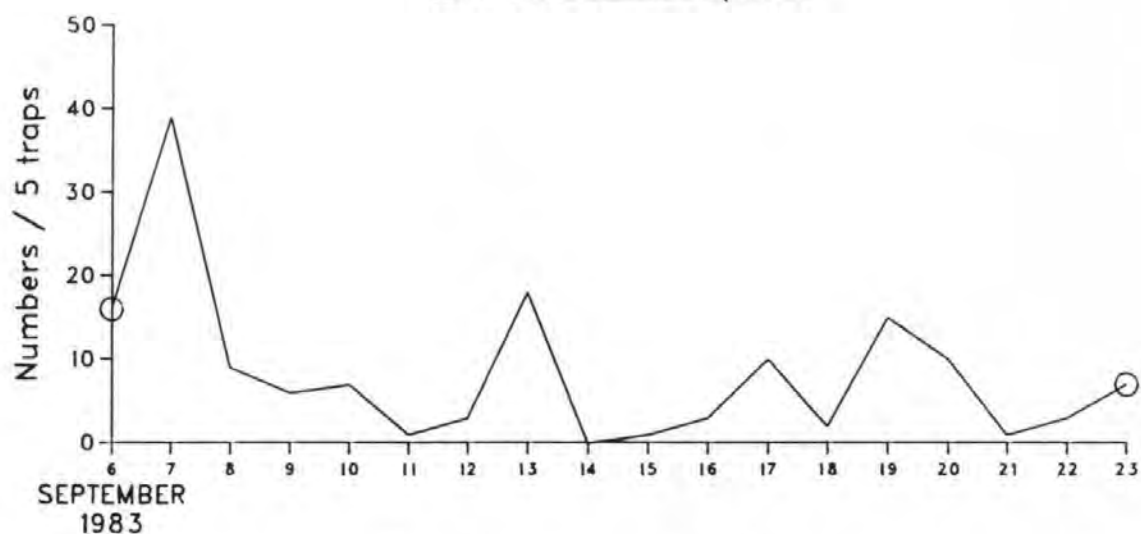
Bembidion lampros

Pterostichus melanarius
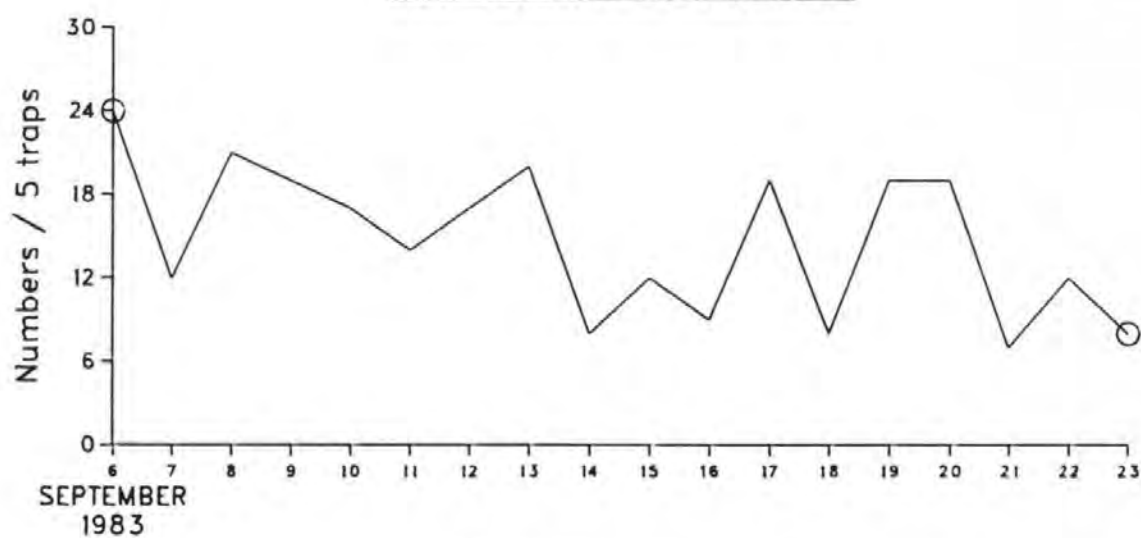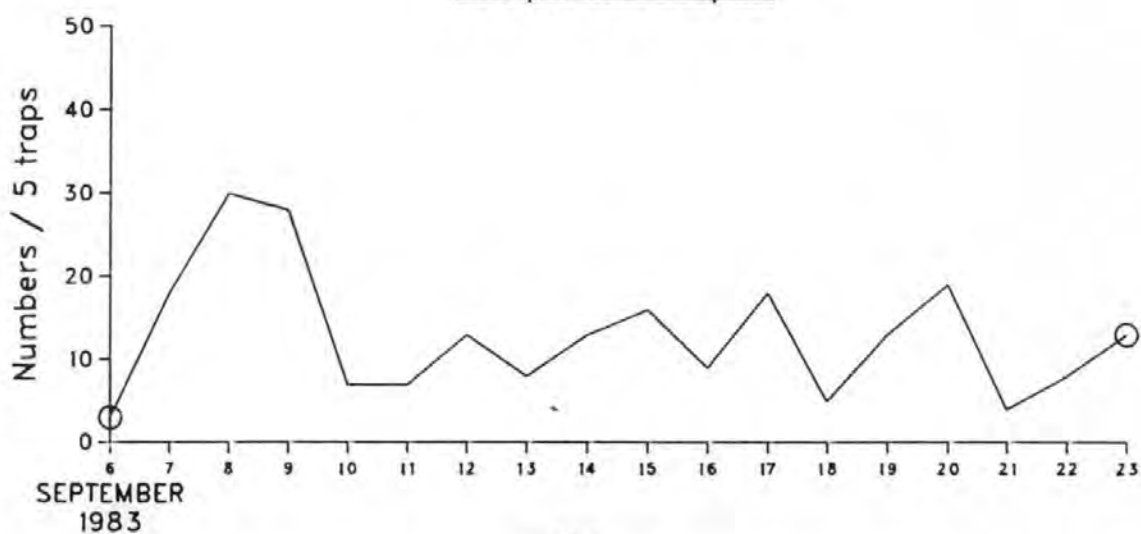
Harpalus rufipes

Minimum temperature

Daily rainfall

Humidity

Wind
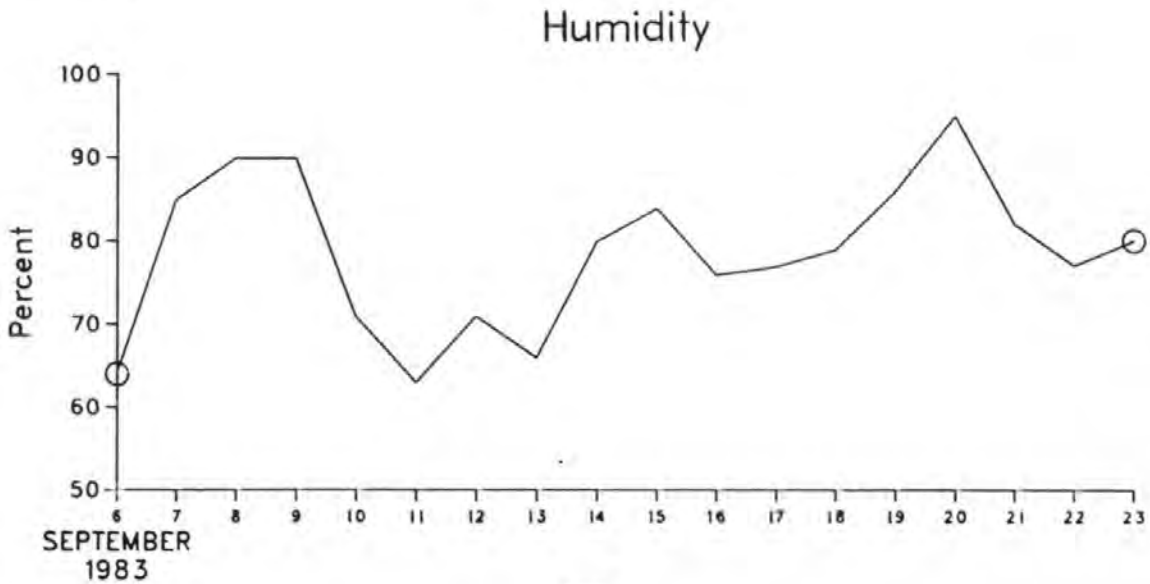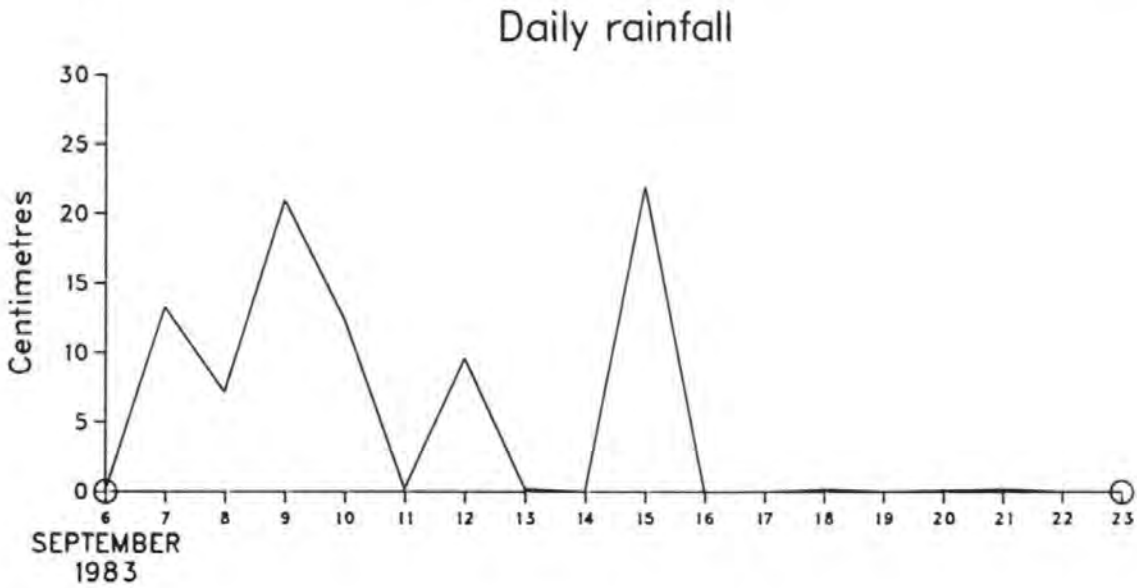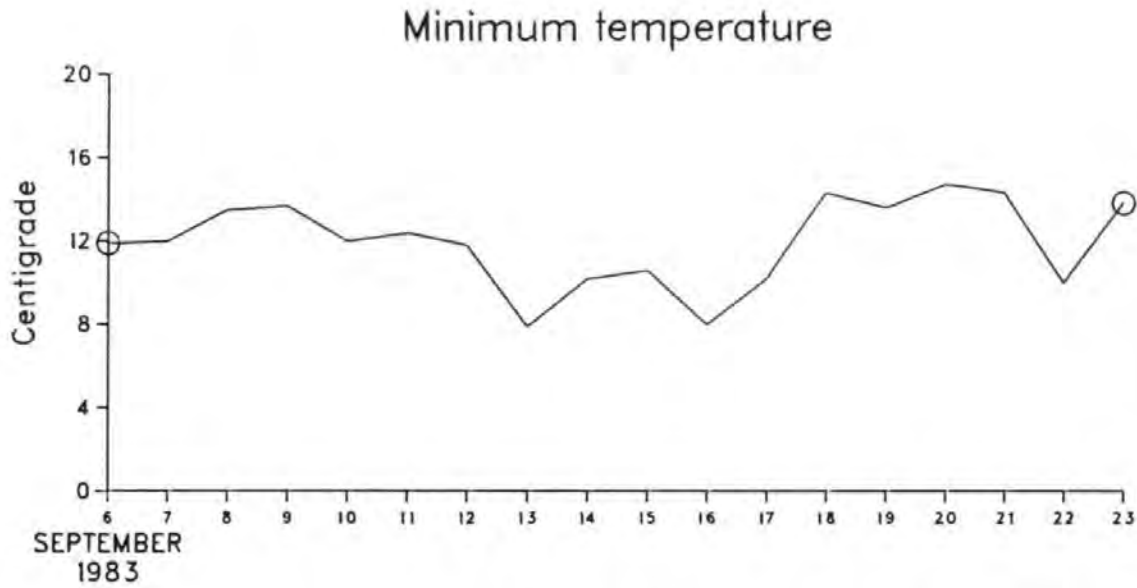
SEPTEMBER
1983
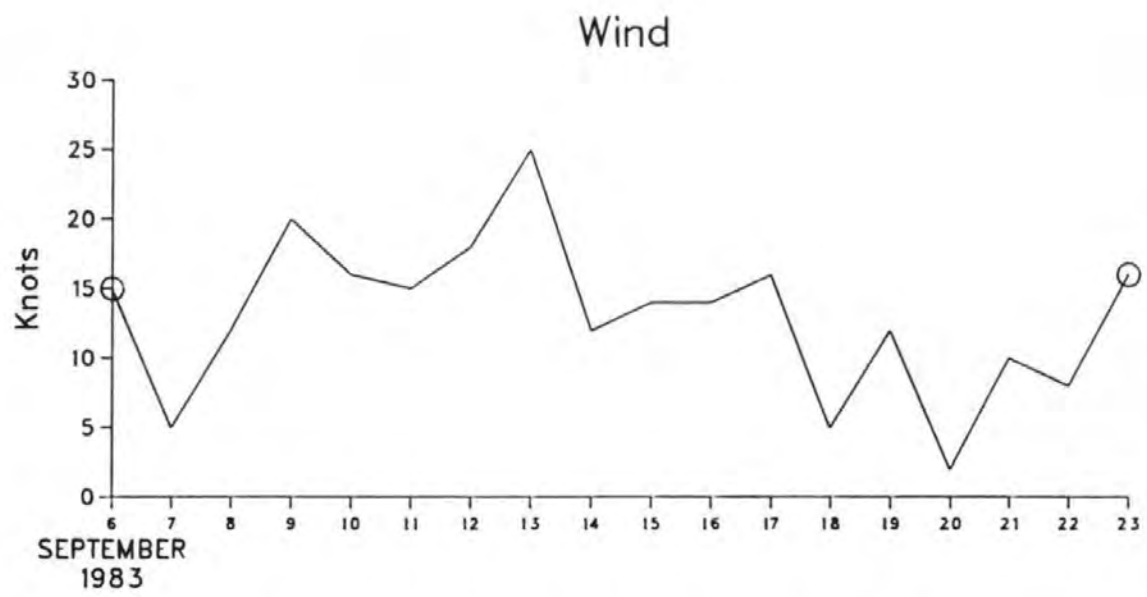
4.3 Meteorological Effects

Meteorological factors can affect carabids in a number of different ways. All carabids have a prefered set of environmental variables such as temperature, humidity and light. These appear to be fairly stable within a species, though there may be differences between the sexes and the prefered conditions may vary at different times of the year or according to the physiological state of the individual (Thiele 1977). Outside the range of conditions to which the beetles are adapted they will become inactive and the extremes which carabids can withstand have been investigated in a number of different studies (see Thiele 1977).

Of the various different factors temperature appears to have the greatest effect and a number of studies have been carried out on the influence of temperature on locomotory activity. Jones (1977) found that the catch of large species (e.g. P. melanarius and H. rufipes) was positively associated with monthly accumulated temperature, whilst the catch of smaller carabids (e.g. N. brevicollis and B. lampros) was negatively associated. Brunsting (1981), studying P. oblongopunctatus found a strong positive correlation of activity with temperature in this species, although the relationship changes over the beetle's period of activity and so cannot be assumed to remain constant. Below a certain temperature carabids become inactive, Jones (1977) finding that P. melanarius and H. rufipes became inactive at less than 5°c, whilst Mitchell (1963a) demonstrated minimum temperatures of 9°c and less than 4°c in B. lampros and T. quadristriatus respectively.

Apart from influencing activity temperature can also affect the development of the larvae and thus influence the timing of the increases in activity and numbers in the spring and early summer as

the adults emerge from pupae. Jones (1979) states that favourable long term temperatures encourage larval development, whilst short term weather encourages activity.

As can be seen from the results there was a great deal of variation in the numbers caught with time during the period of study. Often a number of different species in different areas of the sites would show abrupt changes in catch simultaneously and it was considered likely that an external factor such as temperature was likely to be the cause. Between pages 80-108 there are a number of figures showing the change in a number of meteorological factors over the period of study. The range of dates of the various figures are chosen so that they can be compared directly with the corresponding figures of numbers of carabids caught, and the data is corrected so that it is a mean over the same trapping interval. The data itself is obtained from the Polytechnic's own records, available on computer. Thus the data does not reflect absolutely conditions at the various sites and is most reliable for Staddon Heights as this area is closest to the meteorological station.

No statistical analysis of the data has been attempted. This is because over long periods of time there is no significant correlation of any of the metereological factors with numbers caught. It would be possible to use regression analysis to identify long term trends, however the intention in examining the data is to see whether there are any likely causes for the often substantial changes in numbers caught from day to day. There are many instances in Figs. (4.1-4.26) when the numbers caught change simultaneously for a number of species and in different parts of the site. It is considered that these changes are due to external factors and are not likely to be caused by stochastic variation in the catch. These instances are discussed

in the following paragraphs.

There are many occasions when the changes in numbers caught coincide with increases or decreases in temperature. Examples of this include the peak in catch of N. brevicollis on the 10/6/83 (Figs. 4.3a,c), the sharp drop in P. melanarius 5/9/84 (Fig. 4.14c), the reduction in catch of P. cupreus, P. madidus, P. melanarius and H. rufipes 5/7/85 (Figs. 4.16a,c, 4.17, 4.18) and finally the increase in catch of P. melanarius, H. rufipes, A. aenea and C. fuscipes on the 12/9/85 (Figs. 4.22, 4.23c, 4.25, 4.24).

Previous studies have not found any significant correlation of activity with rainfall or humidity (Jones 1979, Brunsting 1981), though Ericson (1979) showed that rain did prevent activity in P. cupreus on occasion. Similarly it is more difficult to find examples of rain affecting carabid behaviour during the three years of this study. The increase in activity of many species in September 1983 at Battisborough Cross coincides with an increase in rainfall after the dry summer (Figs. 4.1-4.6), and at the same time temperature is declining. At Staddon Heights in 1985 the reduction in a number of species at the beginning of September was caused by heavy rain flooding the traps, and not necessarily by any direct effect on activity. There are a number of occasions when heavy rainfall does not appear to be reflected in any change in catch.

Similarly to rainfall, humidity and wind do not appear to have any correlation with catch.

As a further check on the day to day effect of meteorological influences on activity, the change numbers of three different species, P. melanarius, H. rufipes and B. lampros, during September 1983 is shown in Fig. (4.27). During this period the traps were emptied daily and the corresponding data for temperature, rainfall and humidity is

shown in Fig. (4.28, 4.29). As can be seen there is no correlation of

the numbers caught with these factors, although there are some large

changes in the factors over the period. Again no objective of this

study

has been made, but since the variations in meteorological factors are

not very large it may be that any response by the beetles is hidden by

stochastic variation

One query is whether the changes in catch are due primarily to

changes in abundance or to changes in activity. At times it is

possible to check which of the two is the most important by looking at

the proportion of marked individuals recaptured over the period. If

this proportion remains the same as it was previously during an

increase in catch then this suggests that an increase in activity

ocurred, if, however, it decreases then it is probable that there was

an increase in population density (or mortality of marked

individuals). Conversely during decreases in catch the proportion

marked will increase if there is a fall in abundance. This is similar

to the Lincoln Index method of estimating populations, although no

estimate of numbers is made.

At Staddon Heights in 1984 during the peak and sharp drop of

P. melanarius, at the end of August and beginning of September, the

proportion marked remained relatively constant (though confused by a

number of releases over the period). Thus it appears that the peak

was caused by an increase in activity rather than numbers. After the

middle of September the proportion of recaptures was much lower.

Although it is possible that this due to beetles leaving the trap

grid, in comparison with Staddon Heights 1985 the recaptures ocurred

over a much shorter period. Although the comparison must be made with

great caution, this suggests that it is probable that the decrease in

numbers caught through September is due to mortality or the

beetles becoming dormant.

Similarly the increase in numbers of P. melanarius at Rumleigh in 1985, at the beginning of July, coincides with an increase in recaptures. However the increase at the beginning of August is more complicated and appears to be an increase in both numbers and activity. Here the proportion of recaptures drops at the end of July, but then remains the same through the rest of the peak. Finally the reduction of the same species at Staddon Heights after the 10/9/85 coincides with an increase the proportion of marked recaptures. Thus this is an occasion when the reduction is due to a reduction in the population rather than activity.

In conclusion environmental factors, especially temperature can have a large effect on the numbers of carabids caught. The relationship is not always clear and is dependant on a number of factors, including the physiological state of the carabids (Brunsting 1981, 1983). Some of the large changes in catch appear to be caused by relatively small changes in temperature, often with larger changes in the days before or afterwards which have no effect. It is possible that these changes trigger a response in the beetles, i.e. a sharp drop in temperature towards the end of the season in September may cause a large proportion of the population to become dormant (or die) and so there is a sharp and immediate drop in the numbers caught. However there are many other influences on the numbers of carabids which are captured and the data for September 1983 shows that meteorological effects by themselves can only explain a small part of the variation. It must not be forgotten that stochastic effects will probably cause a large proportion of the changes especially in small trap grids.

4.4 Over-wintering Sites

As has been shown by a number of studies (Sotherton 1984, 1985, Desender 1981, Desender et. al. 1982) some carabids hibernate in the borders of agricultural fields. The advantage of moving to these areas to over-winter is probably an improvement in micro-climatic conditions. Desender et. al. (1981) looked at the micro-climatic variations between the edge and centre of pastures and found that the edge provided a reduction in extremes of temperature and also the minimum temperatures were higher. The difference between the areas was due to the effect of trampling away from the edges. In order to identify these sites a number of soil cores were taken at Battisborough Cross in the winter of 1983/84. The three main different habitats sampled were the field itself, the grassy border and the hedge bank. Attempts were made to sample the track but this proved extremely difficult owing the very hard-packed soil, it is unlikely that it formed an over-wintering site for carabids.

Method

The soil corer used had a diameter of 10.5cm and was 17cm deep. It was forced into the ground with a sledgehammer and the cores placed separately in plastic bags. On returning to the lab the cores were first sorted by hand to remove the majority of the adult carabids. The samples were then placed in Tullgren funnels and left for at least three days, collecting all the organisms in alcohol. In fact no adult carabids were found after treatment in the funnels, all having been found in the hand sorting. Apart from the core samples, larger sod samples were taken from the grassy borders. These measured

approximately 50 x 50cm and were cut out using a spade, to a depth of about 15cm. These were then treated in the same way as the other samples.

Table (4.3) shows the date and site of all the cores taken. All carabids were identified to species, and all other invertebrates classified according to order.

Results and Discussion

Table (4.4) shows that a total of 66 adult carabids (of 13 species) were found. There are clear differences between the various areas, with only two individuals being found in the field and different sets of species in the hedgebank and the grassy borders. In the hedgebank B. lampros ocurred in the highest density ($20.5m^{-2}$) and this appears to be the favoured over-wintering site of this species. Sotherton (1985) also found significantly greater numbers of B. lampros in hedgebanks, although there were also large numbers in other habitats, including grass strips. Of the other species T. quadristriatus has been recorded over-wintering in a hedgerow by Pollard (1968) and A. dorsale has been found in a variety of field boundaries, being least common in grass strips (Sotherton 1985).

The grassy area was dominated by the genus Amara, although a single B. lampros was also caught. Sotherton (1985) found that A. aenea was most abundant in established grassland, whilst A. familiaris and A. plebeja were more common in shelter-belts. In pastures Desender (1982) found that A. aenea was found mainly in the edges. At this site the edge provides the most important over-wintering habitat and, with the exception of a few very rare species, all the Amara species caught in the traps were found in the

Table 4.3: Dates of the different soil cores

Date	Hedge	Field	Edge
	number of cores		
16/11/83	10	20	
11/1/84	10	10	10
19/1/84	10	10	10
10/1/84	10	10	10
15/2/84			5*
Total	41	50	30+5*

*: Sod samples

Table 4.4: Carabids found in soil samples, total number and density

Species	Hedge		Field		Border	
	No.*	#m^{-2}	No.*	#m^{-2}	No.*	#m^{-2}
Loricera pilicornis	1	2.6				
Trechus quadristriatus	5	12.8	1	2.1		
Bembidion lampros	8	20.5			1	1.0
Pterostichus strennus	2	5.1				
Agonum dorsale	2	5.1				
Amara aenea			1	2.1	17	17.5
A. communis					4	4.1
A. familiaris					9	9.3
A. ovata					3	3.1
A. plebeja					2	2.1
Bradycellus verbasci					1	1.0
Demetrias atricapillus					1	1.0
Dromius linearis	1	2.6				

* number of individuals

n.b.. # is used to signify 'no.' in this and following tables

grass strip. It is interesting to note that two species

(A. familiaris and A. communis) which were relatively rare in the

pitfall and gutter traps (Tables 3.2, 3.3) formed a large proportion

of those found in the soil samples. The remaining species, Demetrius

atricapillus, is uncommon in the south-west of England and at

Battisborough Cross was only found in the hedgerow. In other areas

the species migrates away from over-wintering sites at the edge of

fields in the same fashion as Agonum dorsale (Coombes & Sotherton

1986), it is also considered to be an important predator of aphids.

In the field itself very few carabids were found, though a number

of species over-winter there. It is possible that the soil cores were

not sufficiently deep to sample individuals buried in the ground.

Tables (4.5, 4.6) show the total of all the invertebrates found

in the survey, demonstrating that the hedge was the richest both in

terms of numbers and also variation. This is likely to be because of

the relatively well-formed litter layer in this habitat. Many of the

groups form prey for carabids. The grassy border also contained large

numbers of invertebrates, but in contrast the field proved poor with

the exception of a large number of annelids.

With the low numbers of carabids found it is not possible to

identify differences within the three types of habitat sampled even

though, as can be seen from Tables (3.2, 3.3), there were some

differences between the species caught in the pitfalls in Fallow Hedge

and Cabbage Hedge. Although there were a few individuals of N.

brevicollis seen during surface search of the hedgebank and they were

caught in pitfalls during the period, none were found in the soil

cores. One pitfall (Fallow Hedge #5) continually caught large numbers

of this species and a number of cores were taken in the vicinity of

the trap in an attempt to locate over-wintering sites, with no

success. As this carabid is still active in the winter it is possible that individuals could avoid being caught in the soil samples. The majority of larvae found were N. brevicollis and these occurred in similar numbers in both the hedgebank and grass strip.

Although the results are limited they do indicate the importance of the borders of sites such as Battisborough Cross to carabids, and the findings support those of other studies. Sotherton (1984) found that the over-wintering habitats used by a species varied between years and places and it is likely that carabids respond to micro-climatic changes in the different areas (Thiele 1977). This suggests that the pattern at Battisborough Cross might not be consistent and the relative importance of the areas might change.

Coombes & Sotherton (1986) showed that it was possible to relate the density of some carabids in the centre of fields with the numbers found over-wintering in the field edges. However this was not possible in this study, largely because a much more intensive sampling would be necessary in the winter. Early in 1984 gutter traps were placed along the edge of the grass strip in order to sample the beetles leaving the habitat. Unfortunately these were removed by the farmer after only a few weeks and little useful information was obtained. Further details of beetles moving out from the field boundaries are contained in Section 4.5.

Table 4.5: Soil cores, total results

SITE	DATE	NO. of soil cores	Carabids	Staphylinids	Annelids	Isopoda	Chilopoda	Diplopoda	Coleoptera	Acari	Mollusca	Pseudoscorpions	Collembola	Carabid & Staph. larvae	Other larvae
FH	10/11	5	4	13	7	9	15	15	3	5	1			5	1
CH	10/11	5	8	37	2	9	12	11	14	19	2	9		8	4
FIELD	10/11	10	1	1	1	1							1		
CH	11/1	10	6	12	5	38	5	20	32	36		6	1	2	14
FIELD	11/1	10		2	33					2					
EDGE	11/1	10	3	7	63	2	2	2	4	25			3	12	35
FH	19/1	10	2	18	9	9	5	6	10	1		1	1	13	5
FIELD	19/1	10	1		9					1					
EDGE	19/1	10	4	18	65					10	1		2	11	20
FH	30/1	10	1	36	10	18	19	3	42	31		2		4	7
FIELD	30/1	10		1	34								1		
EDGE	30/1	10	1	11	13	5	7	12	2	6				8	5
EDGE	15/2	5*	33	46	269	1		1	13	18			35	38	75

* Sod samples

TABLE 4.6: Density of different groups, number in each square metre

SITE	TOTAL AREA M²	Carabids	Staphylinids	Annelids	Isopoda	Chilopoda	Diplopoda	Coleoptera	Acari	Mollusca	Pseudo-scorpions	Collembola	Carabid & Staph. Larvae	Other larvae
HEDGE	0.35	61	335	95	240	162	159	292	266	9	52	3	90	90
EDGE	0.94	44	87	437	9	10	16	31	53		3	39	74	143
FIELD	0.43	5	9	178	2				7				2	2

4.5 Distribution of Individual Species

At each of the sites a number of species were caught in sufficient quantity to allow further investigation of their distributions. These are all species found in large numbers in the grids of pitfalls in the field but which may also have an association with the field boundaries. Analysis of Variance was used with three factors; Date (i.e. the change in numbers over the weeks of sampling), Line and Row (the two dimensions of the trap grid). Line and Row are two arbitarily chosen terms, Line will be used to refer to the lines of pitfalls which are parrallel to the hedge (if one exists at the site) and these are at various distances from the edge. Row will be used to refer to the lines of traps which are perpendicular to the field edge, at all sites there were five traps in each line and hence five rows.

Details of the statistical method are given in Appendix 1, but briefly all data were summed into weeks and then transformed using a transformation derived from Taylor's Power Law (Taylor 1961). The analysis was carried out on four sets of data; Battisborough Cross 1983, Staddon Heights 1984, Staddon Heights 1985 and Rumleigh 1985, the results being summarised in Tables (4.7a-d). Only data from the pitfall traps is used in the analysis, although records from the gutters may be mentioned in discussing the results.

At Battisborough Cross four species were analysed and the total number of individuals caught in each trap is shown in Table (4.8a-d). Each species is treated seperately below:

Table 4.7:

Summary of the Analysis of Variance

4.7a Battisborough Cross 1983

SPECIES	DATE	LINE	ROW	DATE X LINE	DATE X ROW	LINE X ROW
Nebria brevicollis	****	*		**		****
Bembidion lampros	**	****		****		
Agonum dorsale	****	***		***		
Agonum muelleri	****	****	****	****	*	

4.7b Staddon Heights 1984

SPECIES	DATE	LINE	ROW	DATE X LINE	DATE X ROW	LINE X ROW
Nebria brevicollis	****	**	*	***		**
Trechus quadristriatus	****	*	**	*	*	*
Pterostichus melanarius	****		****	****		

4.7c Staddon Heights 1985

SPECIES	DATE	LINE	ROW	DATE X LINE	DATE X ROW	LINE X ROW
Nebria brevicollis	****	**	*		****	**
Trechus quadristriatus	****					
Pterostichus melanarius	****	****	****			****
Amara aenea	****					

4.7c Rumleigh 1985

SPECIES	DATE	LINE	ROW	DATE X LINE	DATE X ROW	LINE X ROW
Pterostichus cupreus	****	****	****		****	**
Pterostichus madidus	****	****	****	**	****	
Pterostichus melanarius	****	****			****	
Harpalus rufipes	****	****	****	*	****	

Significance levels; *-5%, **-2.5%, ***-1%, ****-0.5%

Table 4.8:

Battisborough Cross 1983

Individual trap totals, with Line and Row totals

4.8a Nebria brevicollis

						LINE
50м	3	5	9	5	28	50
20м	9	21	30	15	21	96
10м	14	28	35	18	27	122
0м	21	9	4	17	5	56
HEDGE	54	1	5	3	18	81
ROW	101	64	83	58	99	405

4.8b Bembidion lampros

37	11	19	8	4	79
10	11	3	24	16	64
6	37	3	5	9	60
6	15	12	5	17	55
4	5	1	5	1	16
63	79	38	47	47	274

4.8c Agonum dorsale

6	12	7	1	7	33
8	12	24	5	6	55
6	13	7	6	16	48
4	5	2	5	2	18
8	1	2	0	4	15
32	43	42	17	35	169

4.8d Agonum muelleri

0	6	10	12	4	32
2	13	13	9	15	52
0	10	5	6	2	23
4	9	14	8	20	55
0	0	0	0	0	0
6	38	42	35	41	162

<u>Nebria brevicollis</u>: Firstly the analyses shows that there was a

significant change in numbers over the trapping

period. This reflects the fact that trapping started before the

species' main period of spring activity and so numbers increased

greatly during the trapping. This change in numbers is significant

for all the species at all the sites analysed and is a reflection of

the prolonged sampling sequences (over a number of months). The

numbers caught at each of the different trap lines (Table 4.8a) also

show a significant difference with most individuals being caught

around 10m-20m into the field. The analyses does not identify a

similar difference in the numbers caught in the trap rows.

The significant interaction between Date and Line suggests that

the distribution of the beetle changes with time. This relationship

is shown in Fig. (4.30a), and it is apparent that activity starts a

few weeks earlier in the hedge and is latest at a distance of 50m into

the field. Lyngby & Nielsen (1980) found a similar situation with the

species in relation to a shelterbelt and suggest that it provided a

suitable over-wintering site for adults and that the centre of

activity shifted into the field later as adults emerged from pupae

situated there. In Section 4.4 the results of soil cores taken in

the various areas of the site are discussed and these show that there

were large numbers of larvae (predominantly <u>N. brevicollis</u>) in the

hedgebank, but very few in the field. Thus the interaction may be the

result of two different processes, the early activity in the hedge is

due to adults which over-wintered there and then move out into the

field. The later peaks are likely to be due to emerging adults which

are mainly centred in the hedge and also move out, though there is

additional emergence in the field.

The analysis does not suggest that there was a similar effect

Figure 4.30a: Nebria brevicollis, Battisborough Cross 1983
Movement away from hedge
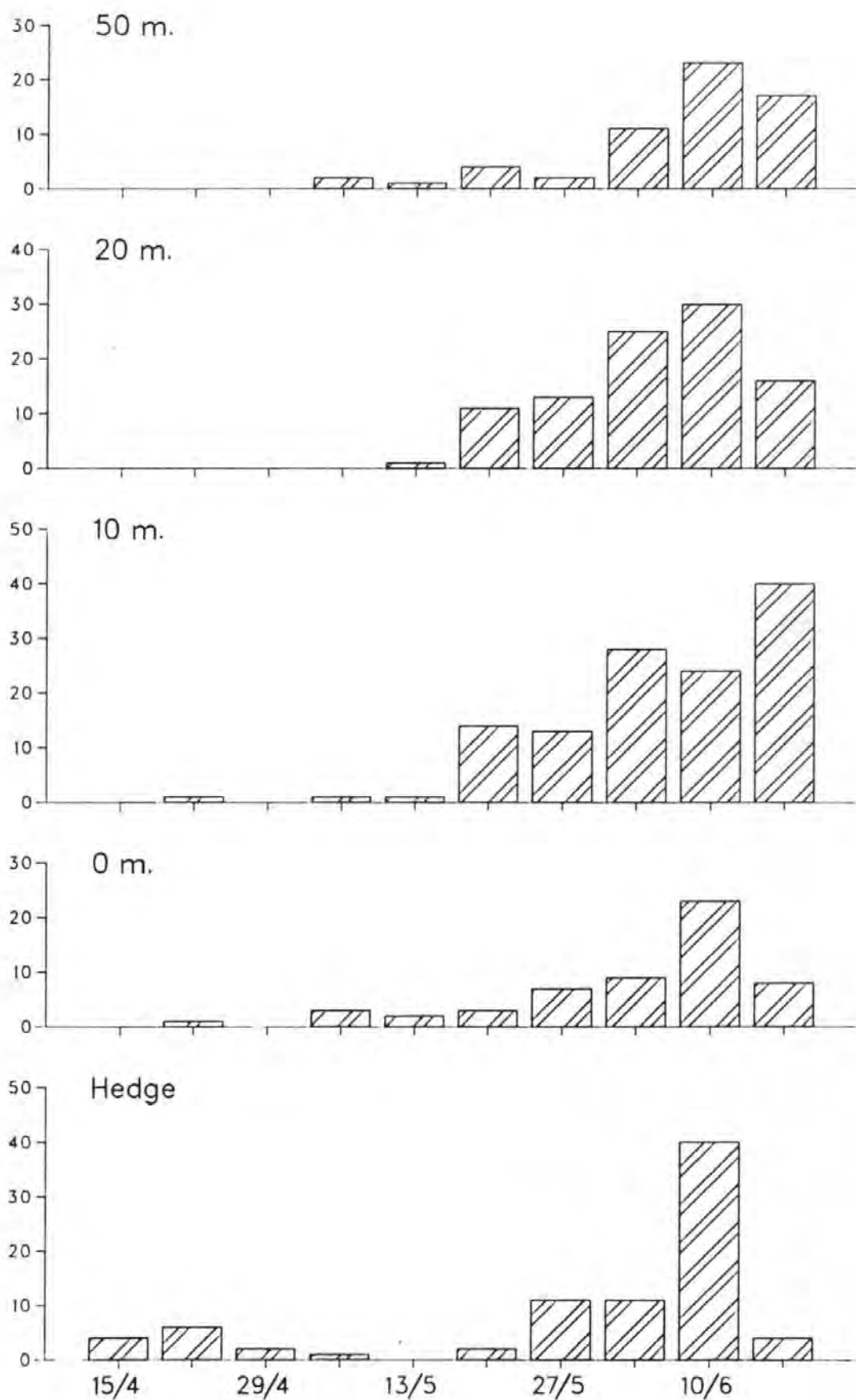
from across the field (i.e. Date x Row interaction). The hedge on this side (Edge Hedge) was similar to Cabbage Hedge, though it was more overgrown. Possibly the wide grass strip made it less attractive as an over-wintering site for this species. The final interaction (Line x Row) is produced by an apparent gradient across the pitfall grid, from trap #1 to trap #25. None of the other species showed a similar pattern and there was no evidence for a change in habitat accross the site, and so the interaction does not appear to have any biological significance.

Pollard (1968) and Jones (1976) found an increase in numbers caught in and close to the hedge, but the situation is apparently different at this site as larger numbers were caught inside the field.

<u>Bembidion lampros</u>: This species shows a similar pattern to the previous one, although activity started earlier in the spring. There is a significant increase in numbers over the trapping period (Fig. 4.1). As mentioned earlier it is a spring breeder and is known to over-winter in field boundaries, particularly hedgebanks (Sotherton 1985). The analyses and Fig. (4.30b) show that there is a wave of movement away from over-wintering sites in the hedge, with peaks occurring at progressively later dates further into the field, confirming the results found by Wallin (1985). The difference between the pattern shown by this species and the previous one is that in <u>B. lampros</u> all the individuals involved are adults from the previous year and move away from the main over-wintering site in the field edges, whilst in <u>N. brevicollis</u> there are many newly emerged individuals in the field.

Table (4.8b) shows the individual trap and line totals. As with <u>N. brevicollis</u> significantly more are found in the field than in the

Figure 4.30b: <u>Bembidion lampros</u>, Battisborough Cross 1983
                     Movement away from hedge
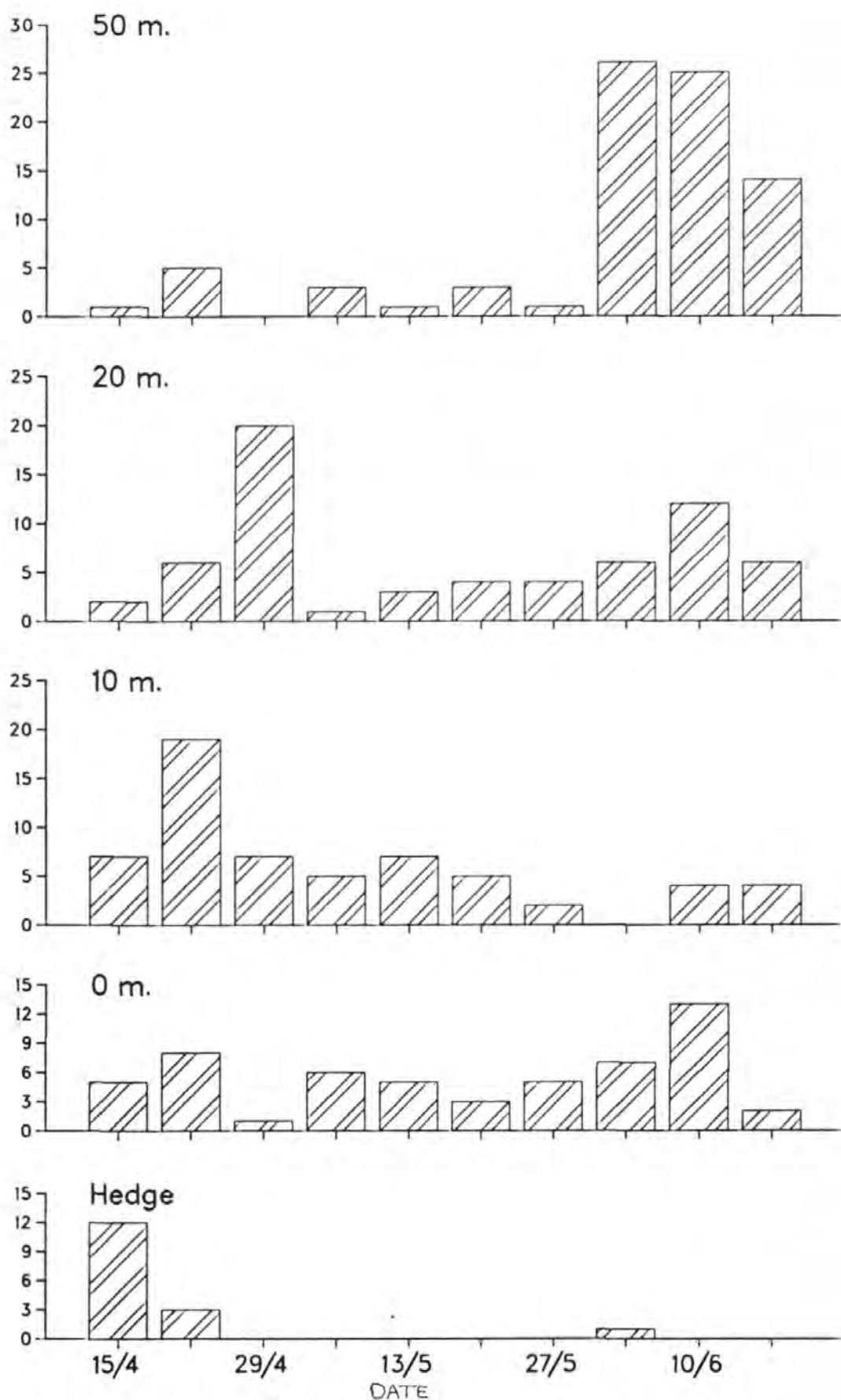
hedge. The low catch in the hedge may be due to the greater amount of vegetation around the traps or may be due to a real difference in behaviour in that B. lampros moves directly away from the hedge into the field with very little activity in the hedge itself.

The other factors are not significant and again it should be noted that there is no Date x Row effect. Although Southerton (1985) found large numbers of the species in grass borders, in this study (Section 4.4) considerably more individuals were found in the hedgebank than in the grass border. Thus any movement away from over-wintering sites would be primarily away from the hedge.

Agonum dorsale: As might be expected from a species with a similar

life cycle, A. dorsale shows the same pattern as B. lampros. Although activity in the hedge commences at about the same time, spread into the field is delayed by a few weeks. Significantly more individuals were captured in the field rather than at the edge or boundary, which may be due to directed movement away from the hedge.

Spread of individuals away from over-wintering sites in hedges has been demonstrated by Pollard (1968) and Sotherton (1982). This last author found a delay of three weeks between peak of activity at the edge of the field and that at distances of 50m or more from the boundary, the dates at Battisborough Cross are broadly in agreement with this (Fig. 4.30c).

Compared to B. lampros where there was an immediate increase in the field (i.e. at 0m, 10m and 20m) after the increase in the hedge, there is a marked delay in A. dorsale. Similar results are presented by Southerton and this suggests that the species may not move directly into the crop, though activity in the hedgerow is low. Intensive

Figure 4.30c: Agonum dorsale, Battisborough Cross 1983
Movement away from hedge
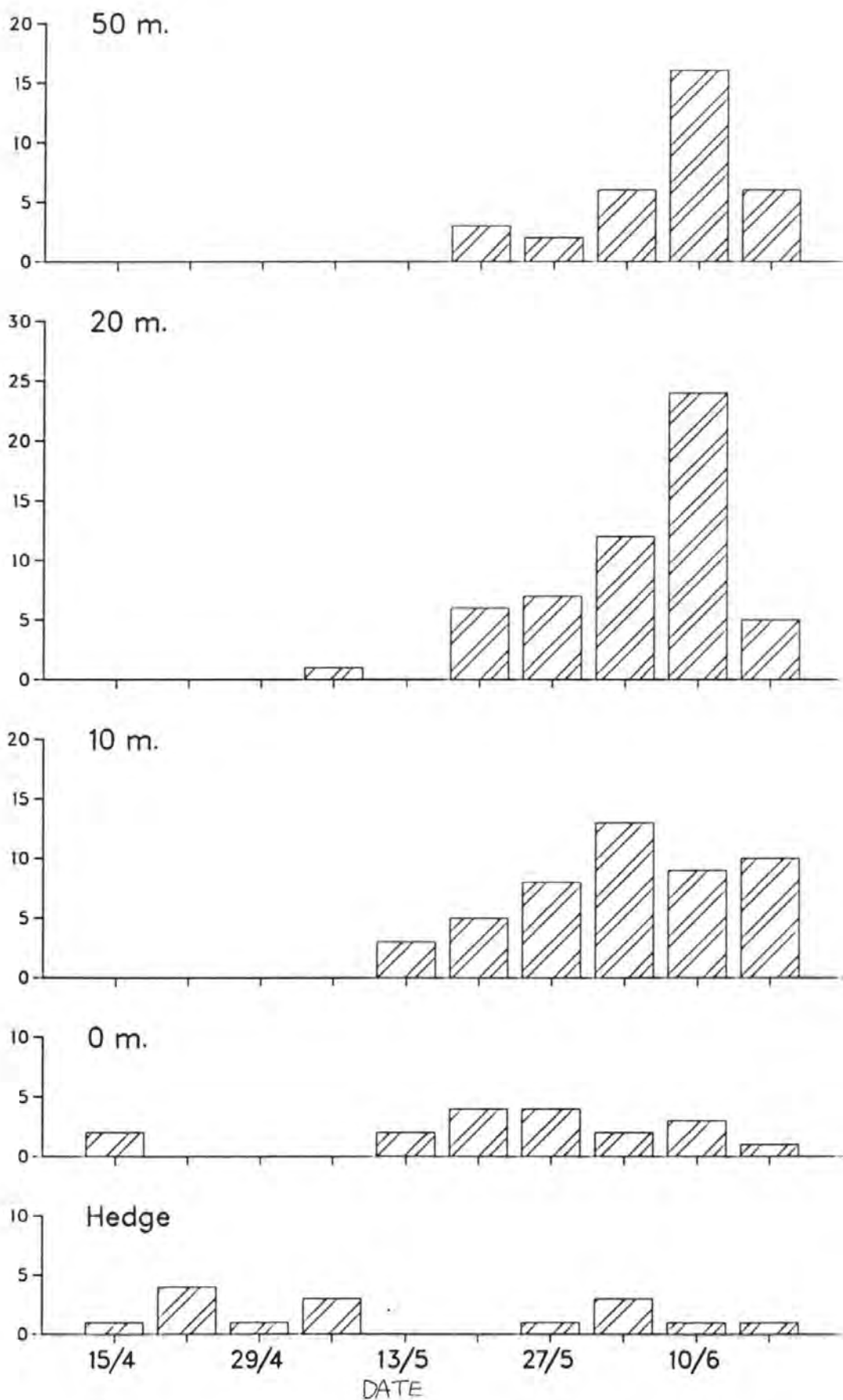
individual mark/recapture studies would be necessary to identify whether this is a real phenomenon. Again there is no effect of traps across the field.

Agonum muelleri: This species shows a rather different pattern to those mentioned above. The results of the Analysis of Variance are shown in Table (4.7a) and Figs. (4.31, 4.32) illustrate the effect of the field boundaries. Activity changes significantly with time, none being caught at the beginning of the trapping period and increasing until the end. Compared to the previous species this one commences activity about 6 weeks later.

There are significant differences between both Line and Row totals. Unlike the other species, A. muelleri was not found in the hedgebank itself, very few individuals being caught in this habitat over the two years at Battisborough Cross. Most individuals were captured at the field edge and at at 20m, whilst few were found in the traps furthest from Edge Hedge. Both the Date x Line and Date x Row interactions are significant, suggesting that there is movement away from the field edges (though not from the hedges). Figs. (4.31, 4.32) show that activity commences first at the edge of the field parrallel to Cabbage Hedge (i.e. 0m) and also at the traps parrallel to Edge Hedge (i.e. Row #5). As with previous species a wave of beetles then moves out into the field.

The pattern of captures suggests over-wintering sites in the grassy borders of the field. Although none were found in core samples taken during this study, Desender (1982) found that the species was an important constituent of the over-wintering population at the untrampled grassy edge of a pasture site. None were found in the pasture itself during the study.

Figure 4.31: Agonum muelleri, Battisborough Cross 1983
Movement away from edge of hedge
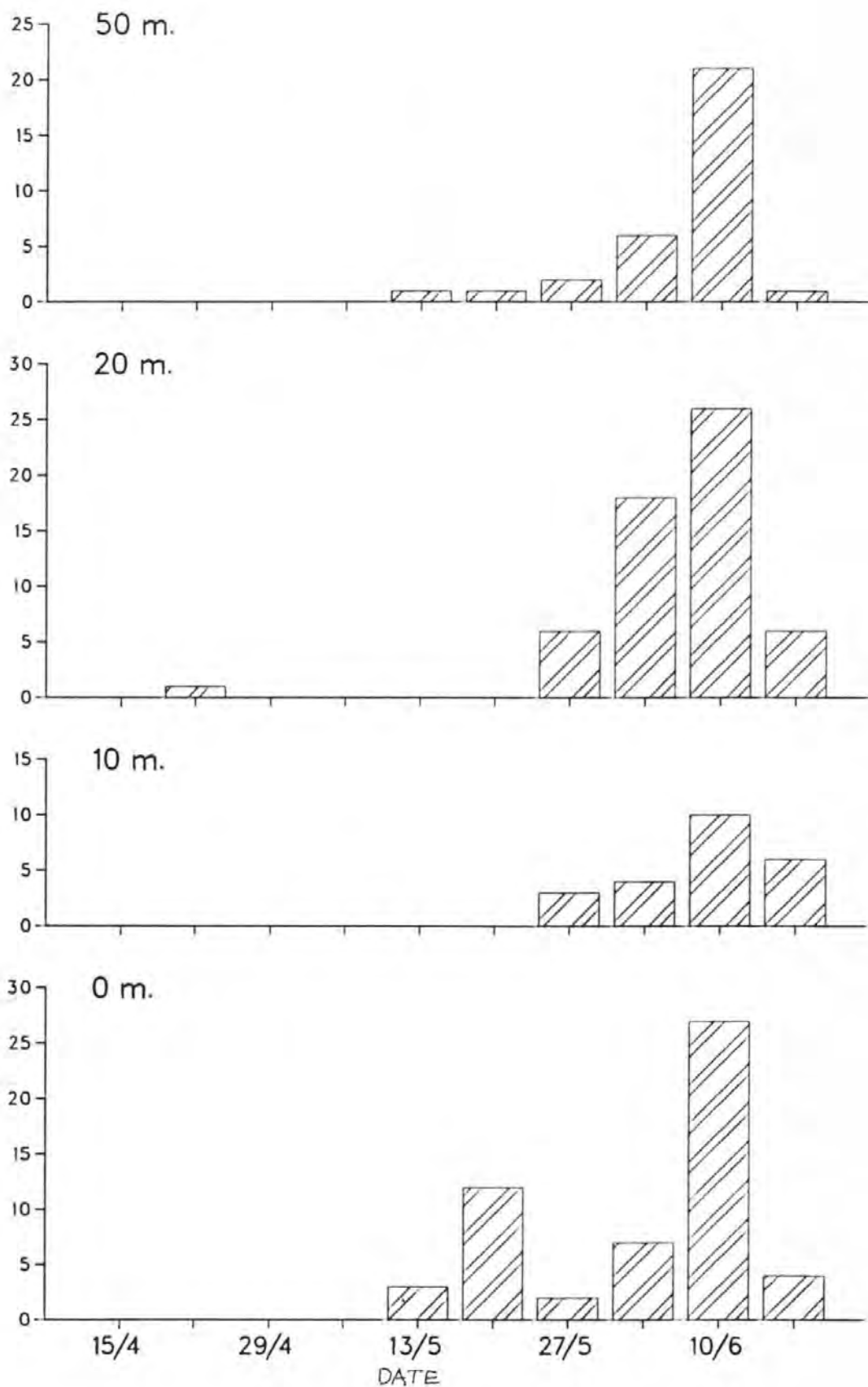
Figure 4.32: Agonum muelleri, Battisborough Cross 1983
Movement away from grassy edge
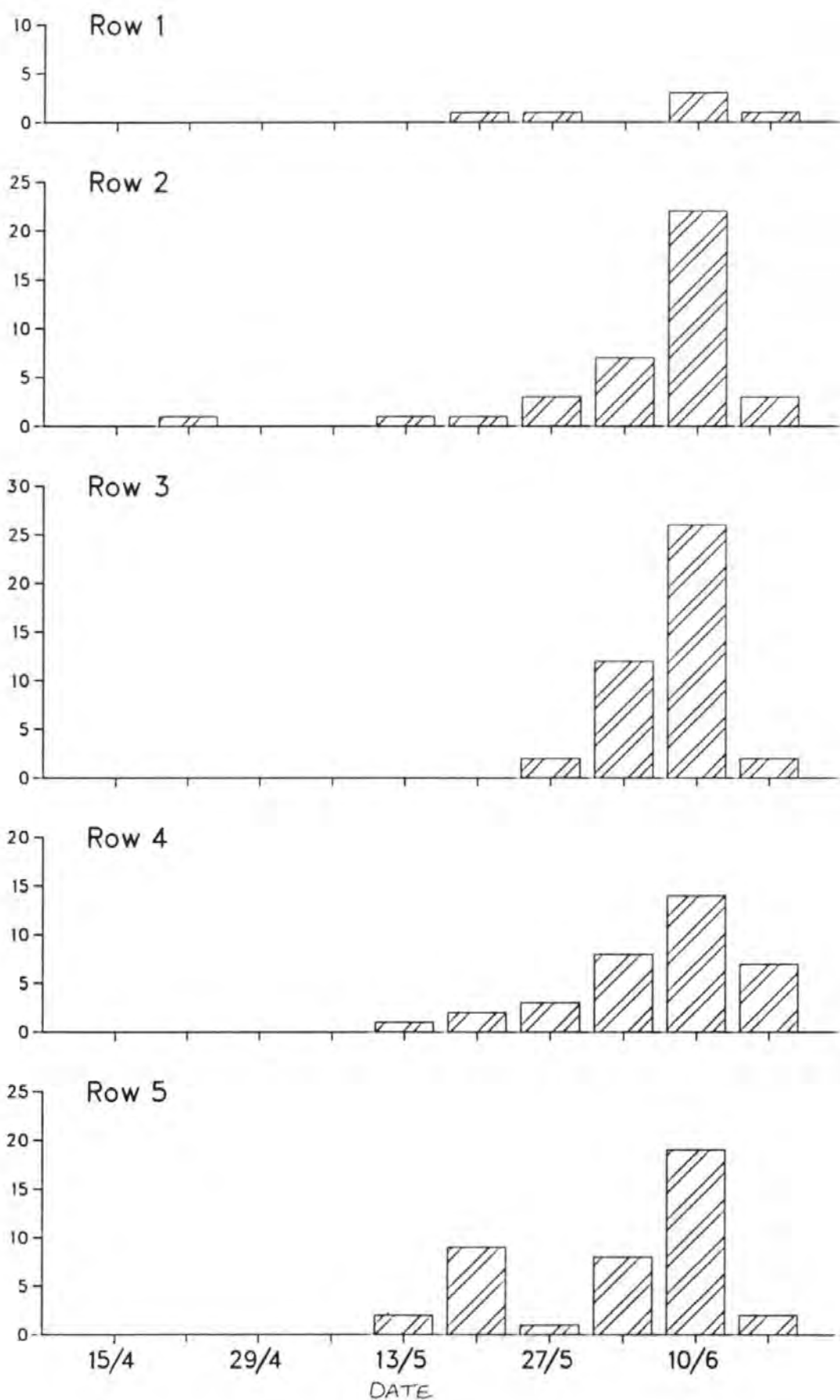
At Staddon Heights in 1984 Analysis of Variance was carried out on three different species; P. melanarius, N. brevicollis, and T. quadristriatus. The results are shown in Table (4.7b), whilst the totals of each individual trap is shown in Tables (4.9a-c). Each species is described below.

Nebria brevicollis: The results from this site provide an interesting comparison to those of Battisborough Cross, as they cover the autumn period of activity rather than the spring. This covers their period of reproduction and individuals were appearing from aestivation rather than over-wintering sites. Activity occurred for a much longer period than in the spring, with individuals being caught continually through the winter.

Each of the factors is significant in the analysis. The effect of Date is due to the fact that at the beginning of the trapping the beetles are still inactive and numbers increase in September. As in the studies of Pollard (1968) and Jones (1976) greater numbers were caught in the hedge and adjacent traps, though large numbers were still found in the field. The significant effect of Row reflects the higher catches in rows #1 and #4, perpendicular to the hedge.

The interaction terms Date x Line and Date x Row illustrated in Figs. (4.33, 4.34). Activity commences earlier in the hedge, at the beginning of September, than it does at greater distances from it and at 35m away numbers increase in early October. This may be due to beetles choosing the hedge as an over-summering place and then migrating away in a similar fashion to the spring movement. Activity remains highest in the hedge and close to it, presumably conditions in this restricted. An alternative is that the beetles aestivate in all areas, though in greater numbers near the hedge, and conditions are

Table 4.9:

Staddon Heights 1984; Individual trap totals, with line and row totals

4.9a Pterostichus melanarius

						Total
30m	80	54	58	57	38	287
25m	89	51	42	41	41	264
20m	77	46	42	30	57	252
15m	73	69	50	38	64	294
10m	62	60	63	42	53	280
5m	50	49	50	51	39	239
Hedge	30	17	32	18	45	142
Total	461	346	337	277	337	1758

4.9b Nebria brevicollis

35m	124	101	52	80	58	415
30m	97	64	68	134	60	423
25m	88	60	20	117	79	364
20m	120	55	51	61	93	380
15m	59	99	103	64	65	390
10m	81	53	50	128	48	360
5m	94	127	114	95	145	575
Hedge	148	182	97	179	153	759
Total	811	741	555	858	701	3666

4.9c Trechus quadristriatus

35m	12	8	10	8	65	391
30m	13	13	6	12	7	51
25m	7	7	2	16	6	38
20m	3	14	3	7	16	43
15m	12	12	8	18	4	54
10m	10	12	10	15	5	52
5m	12	10	16	18	9	65
Hedge	19	8	2	3	4	36
Total	88	84	57	97	65	391

such that those in the hedge break aestivation before those in the field. However it is difficult to envisage micro-climatic differences between these areas which could cause this as, for instance, temperatures are likely to remain higher in the hedge.

The Date x Row interaction is barely significant but Fig. (4.34) shows that activity commences in row #5 before the other side of the grid and then decreases as numbers in row #1 remain high. Row #5 was some 30m away from the adjoining permanent pasture and possibly beetles moved away from this area as an aestivation site.

The final significant effect, Line x Row, suggests a gradient across the grid of traps. There is no evidence for any micro-habitat changes in the crop forming a gradient and it is not considered that any biological significance should be attached to the result.

Pterostichus melanarius: There was an increase in numbers caught in
                        the first few weeks of sampling at this
site but then numbers dropped dramatically and few were captured after the middle of September. The change in numbers caught is illustrated in Fig. (4.14a) and is shown to be significant by the stastistical test.

In contrast to N. brevicollis fewest individuals were captured in the hedge, the analysis showing that significantly more were found in the field. As mentioned in earlier sections it is known to be a field species with no requirement for an alternative site. There is also a significant difference between the various rows, with row #1 catching the greatest number, as with the previous species, though in P. melanarius row #4 catches the fewest.

There is also a significant Date x Line interaction (illustrated in Fig. 4.35). This is caused by the prolonged activity in the hedge,

Figure 4.33: Nebria brevicollis, Staddon Heights 1984
Date x Line relationship
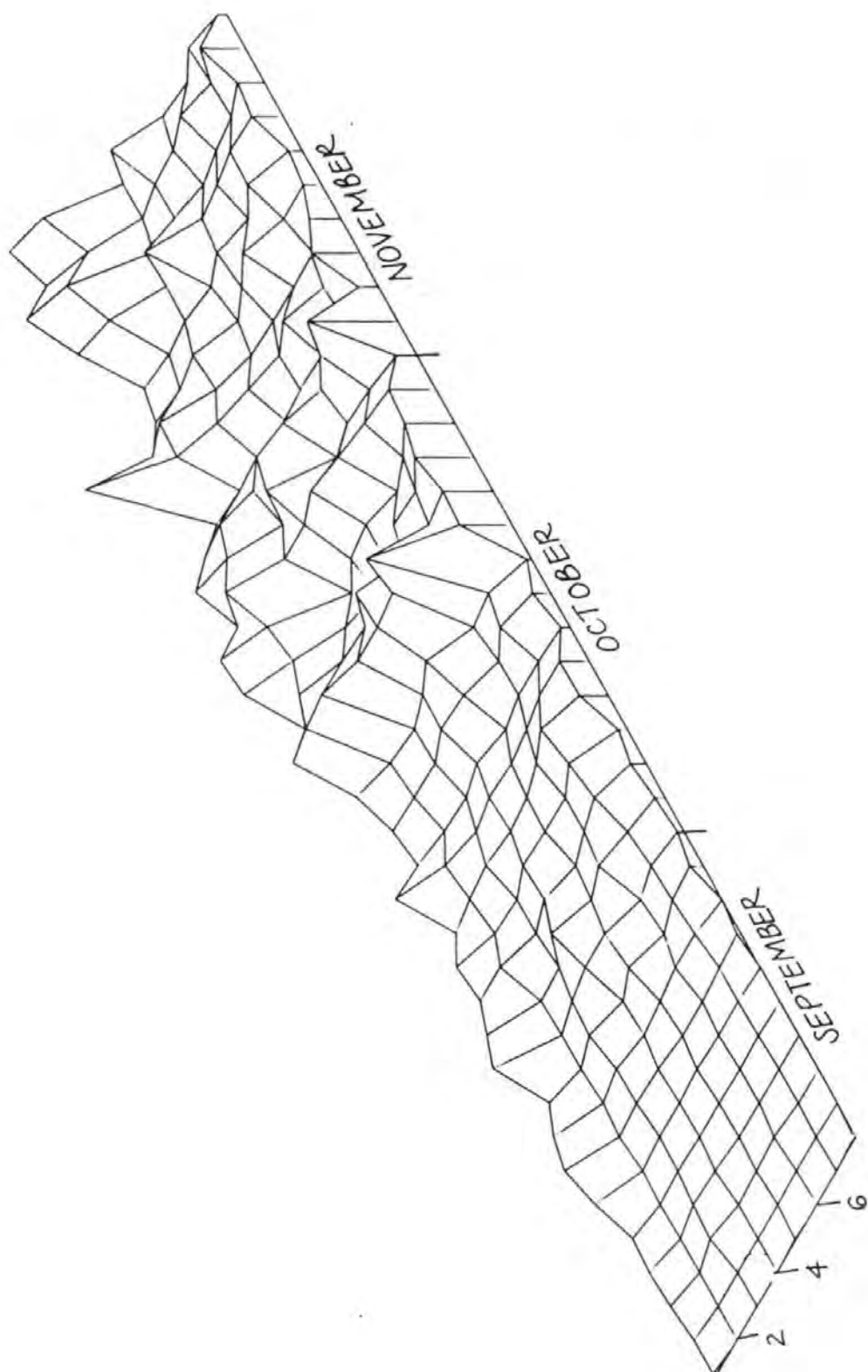
Figure4.34: _Nebria brevicollis_, Staddon Heights 1984
Date x Row relationship
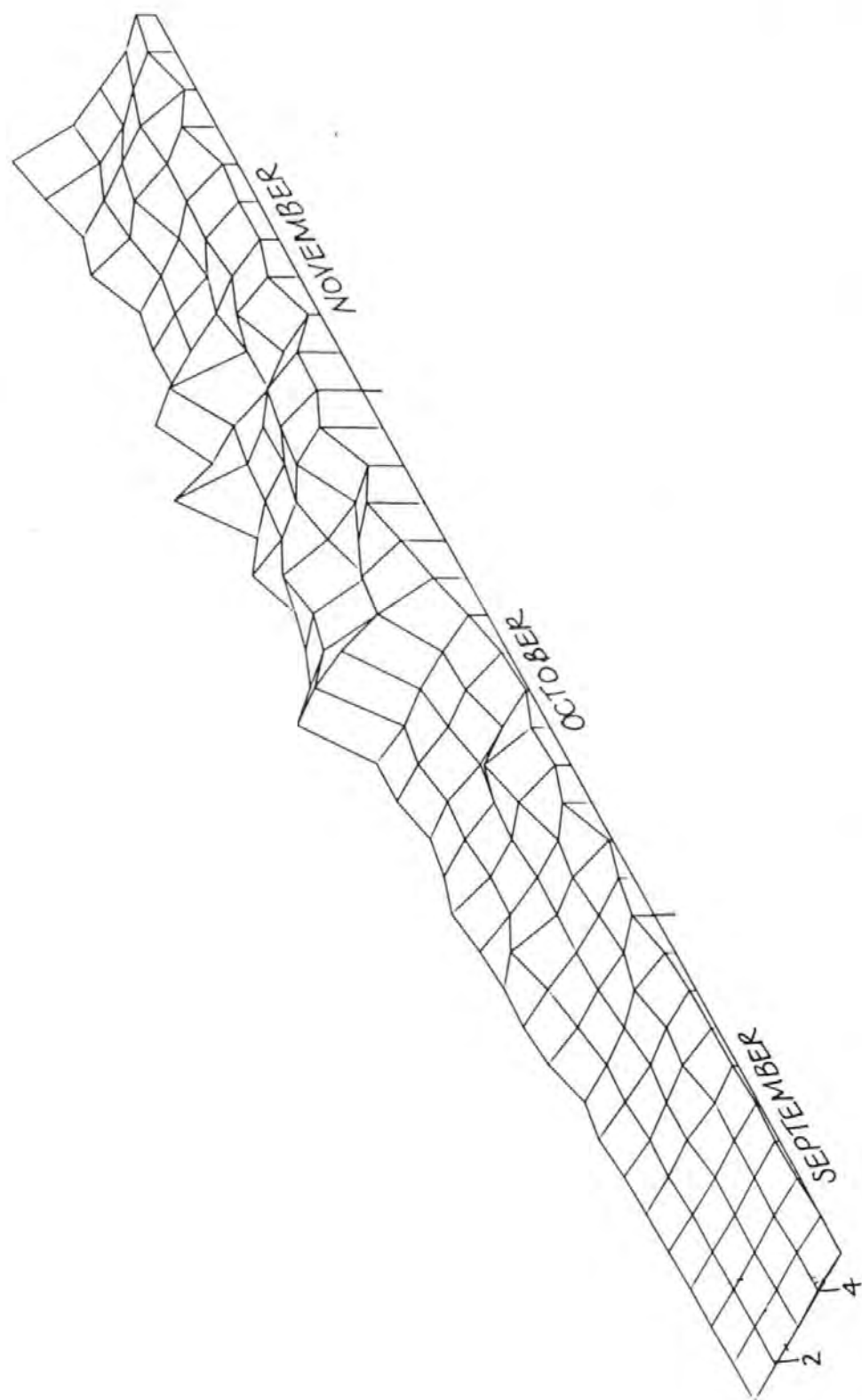
which continued after the numbers in the field dropped to very low levels. During August and September the hedge traps accounted for only 5-10% of the total catch, in October this rose to between 25-50% whilst in November the majority of catches were in this zone. Lyngby & Nielsen (1982) consider it likely that species such as P. melanarius utilise hedges and shelterbelts as over-wintering sites, though the majority stay in the field. There is also a micro-habitat effect with temperatures remaining higher in the hedges, allowing activity to continue later into the winter. Thus the relationship of this species with the field boundaries is different to that found with B. lampros or A. dorsale.


Trechus quadristriatus. Though caught in lower numbers than the two previous species the analysis shows the same pattern as N. brevicollis. Fig. (4.14c) shows that activity increased at the begining of the trapping period, reaching a peak at the end of October. The greatest number were found near the hedge, though not in it, and the analysis shows that the differences between the totals are significant. There are also significant differences between the rows of traps, with row #4 catching the most.

The Date x Line interaction is illustrated in Fig. (4.36) and shows a similar pattern to N. brevicollis. Activity is highest in the hedge during September and then increases in the field. Unlike N. brevicollis this species does not not have a period of aestivation, although it is an autumn breeder with oviposition ocuring from September and into the winter (Mitchell 1963a). Jones (1979) found an increase in the autumn in a winter wheat crop and reproductive activity must account for the increase at this time of the year. It's whereabouts before this is unknown though the results from Staddon
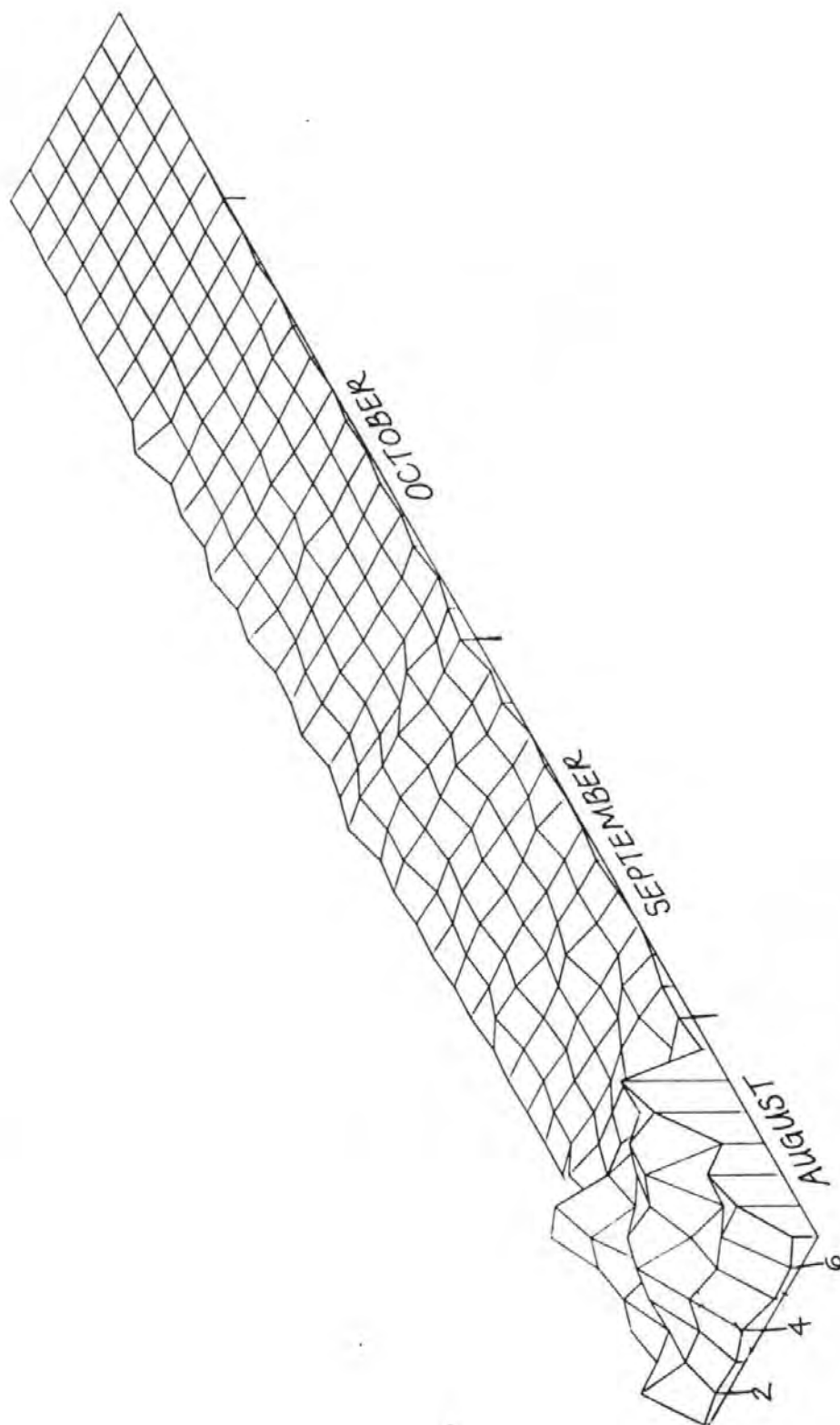
Figure 4.36: Trechus quadristriatus, Staddon Heights 1984
Date x Line relationship
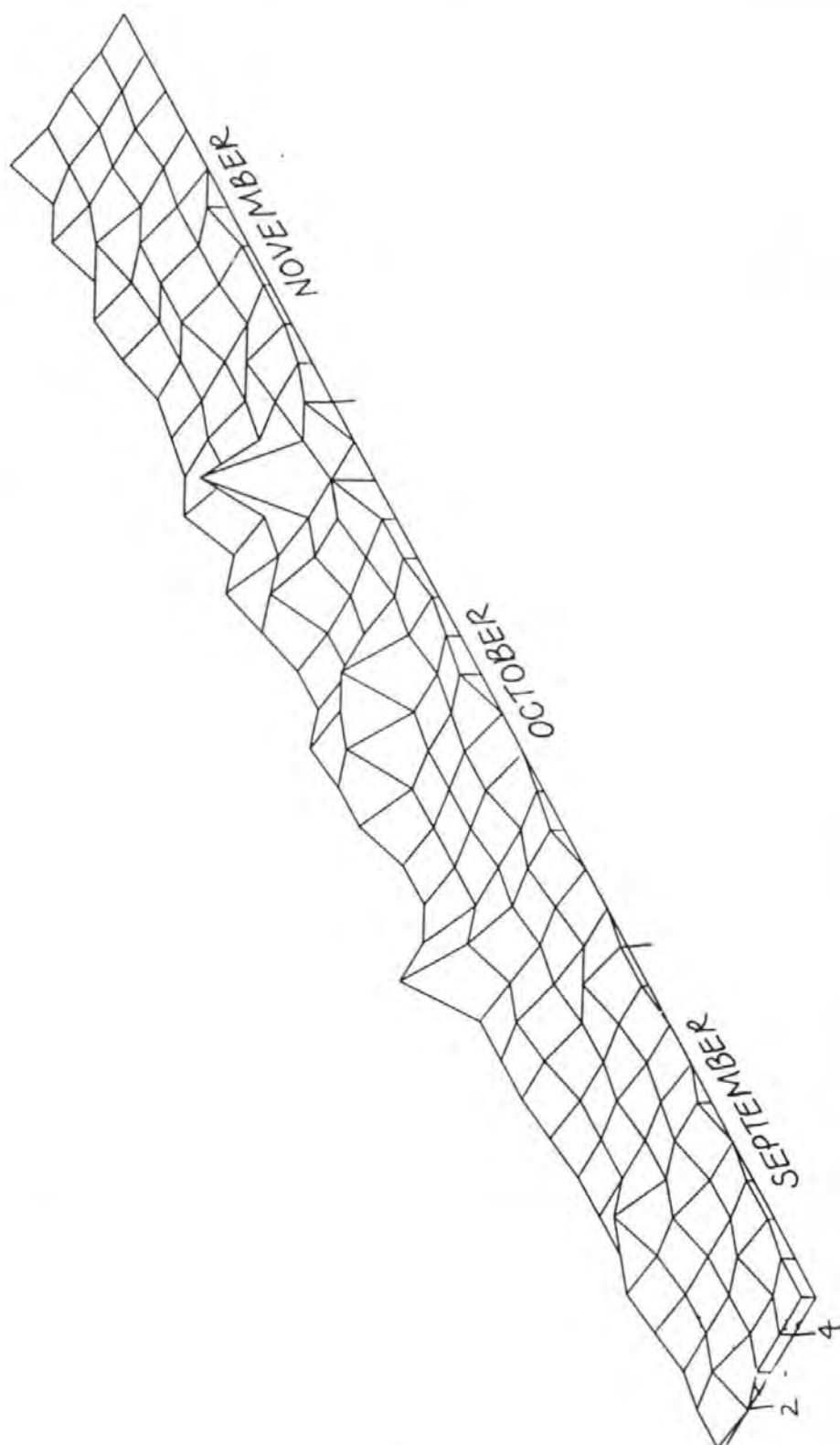
Heights suggest that it is possible that a proportion were inactive in the hedgerow and other field boundaries.

The Date x Row interaction (Fig.4.37) shows the opposite pattern to N. brevicollis with larger numbers captured in row #1 at the begining of the trapping session. Further work needs to be carried out in order to elucidate these interactions. The Line x Row factor is also the opposite of N. brevicollis, with large numbers being caught in row #1 at 35m and few in the hedge in row #5. No particular importance is attached to this.

The following year, 1985, at the different field Analysis of Variance was caried out on the same three species, with the addition of Amara aenea. The trapping period is similar but there was no hedge forming a boundary and the traps were at least 20m from the edge of the field. The results are contained in Table (4.7c) and the results from the traps (both pitfall and gutter traps, though only pitfalls were used in the analysis) in Tables (4.10a-d).

Nebria brevicollis: As at the previous site the main period of activity did not commence until the end of September and the analysis shows that the changes over time are significant. The different numbers caught in the various lines and rows of traps, significant in both, are a reflection of heterogeneity in the crop rather than responses to field boundaries, as has been the case at previous sites. This issue will be covered in greater detail in Section 4.6, where the results from crop and weed cover estimates are presented.

The interaction between Date x Line (Fig. 4.38) shows that numbers increased in the traps in the 50m line at the end of September

Table 4.10

Staddon Heights 1985; Individual trap totals

4.10a <u>Nebria brevicollis</u>

	G*		Pitfalls				TOTAL
50m	69	6	10	7	9	16	48
40m	29	2	14	4	5	1	26
30m	34	7	17	11	7	6	48
20m	80	7	8	6	2	2	25
10m	72	7	8	6	2	2	25
0m	30	4	6	4	5	9	28
	G	49	25	27	12	25	
TOTAL		37	63	33	33	35	

4.10b <u>Pterostichus melanarius</u>

	G						TOTAL
50m	255	22	19	21	24	32	118
40m	105	30	13	19	5	13	121
30m	186	24	35	42	42	24	167
20m	302	35	48	61	48	47	239
10m	240	43	40	95	67	80	325
0m	143	9	45	98	54	64	270
	G	37	84	87	42	79	
TOTAL		163	200	336	248	293	

*G - Gutter traps

Table 4.1∅ cont.

4.1∅c Trechus quadristriatus

	G						TOTAL
5∅m	15	7	7	7	15	7	43
4∅m	9	18	1∅	15	25	8	76
3∅m	5	25	14	9	11	9	68
2∅m	2	9	5	21	29	15	79
1∅m	2	13	6	1∅	5	13	47
∅m	7	19	5	11	6	4	45
	G	11	7	3	1	3	
TOTAL		91	47	73	91	56	

4.1∅d Amara aenea

	G						TOTAL
5∅m	15	5	7	4	12	7	35
4∅m	7	6	7	9	5	12	39
3∅m	13	5	1∅	11	7	5	38
2∅m	17	6	9	7	1	7	3∅
1∅m	23	1	5	2	5	2	15
∅m	19	2	2	5	4	5	18
	G	16	9	3∅	9	21	
TOTAL		25	4∅	38	34	38	

Figure 4. 38: Nebria brevicollis, Staddon Heights 1985
Relationship between Date x Line
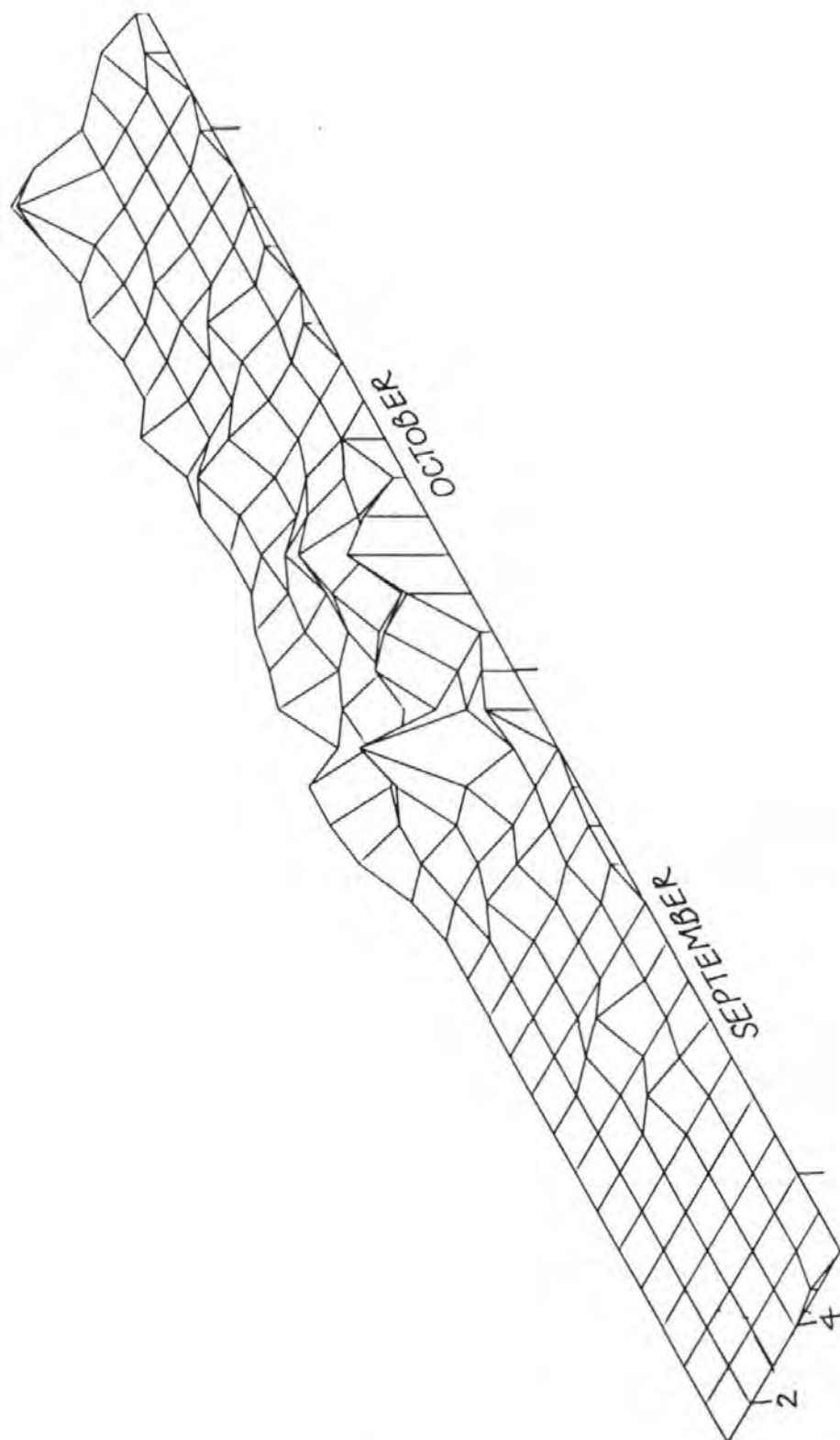
prior to increases in the other parts of the field. By the end of October more individuals were captured in the 0m line. The interaction Date x Row is not significant, however this is illustrated in Fig. (4.39) and it is apparent that towards the end of the trapping period larger numbers are caught in row #1, which was closest to the pasture.

It was mentioned above that there was a great deal of heterogeneity in the crop, and it is probable that the Date x Line interaction is caused by beetles tracking changes in the crop as it develops. The traps at 50m were some 150m away from the end of the field, where there was a strip of ungrazed rough grass 30m wide followed by a hedge. It seems improbable that these could have any influence at such distances. There is no evidence for any beetles moving away from over-summering sites in the adjoining pasture as this would create a significant Date x Row effect, a Date x Line effect in the opposite direction to that observed and also one would find gutter traps catching N. brevicollis before the field pitfalls (Fig. 4.21).

However gutter traps do maintain catches later in the season than the pitfalls and it is possible that the pastures do provide a potential over-wintering site. The same effect could be caused by micro-climatic differences.

Pterostichus melanarius : This species was by far the most numerous in pitfalls at the site, although the numbers caught varied greatly, with activity continuing at high levels until mid-October, Fig. (4.22). These changes are significant as is shown by the analysis, and differ from those at Staddon Heights 1984 in that activity continued at high levels until later in the year. The factors Line and Row both have significant effects and, as with

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Figure 4.39: Nebria brevicollis, Staddon Heights 1985
Date x Row relationship
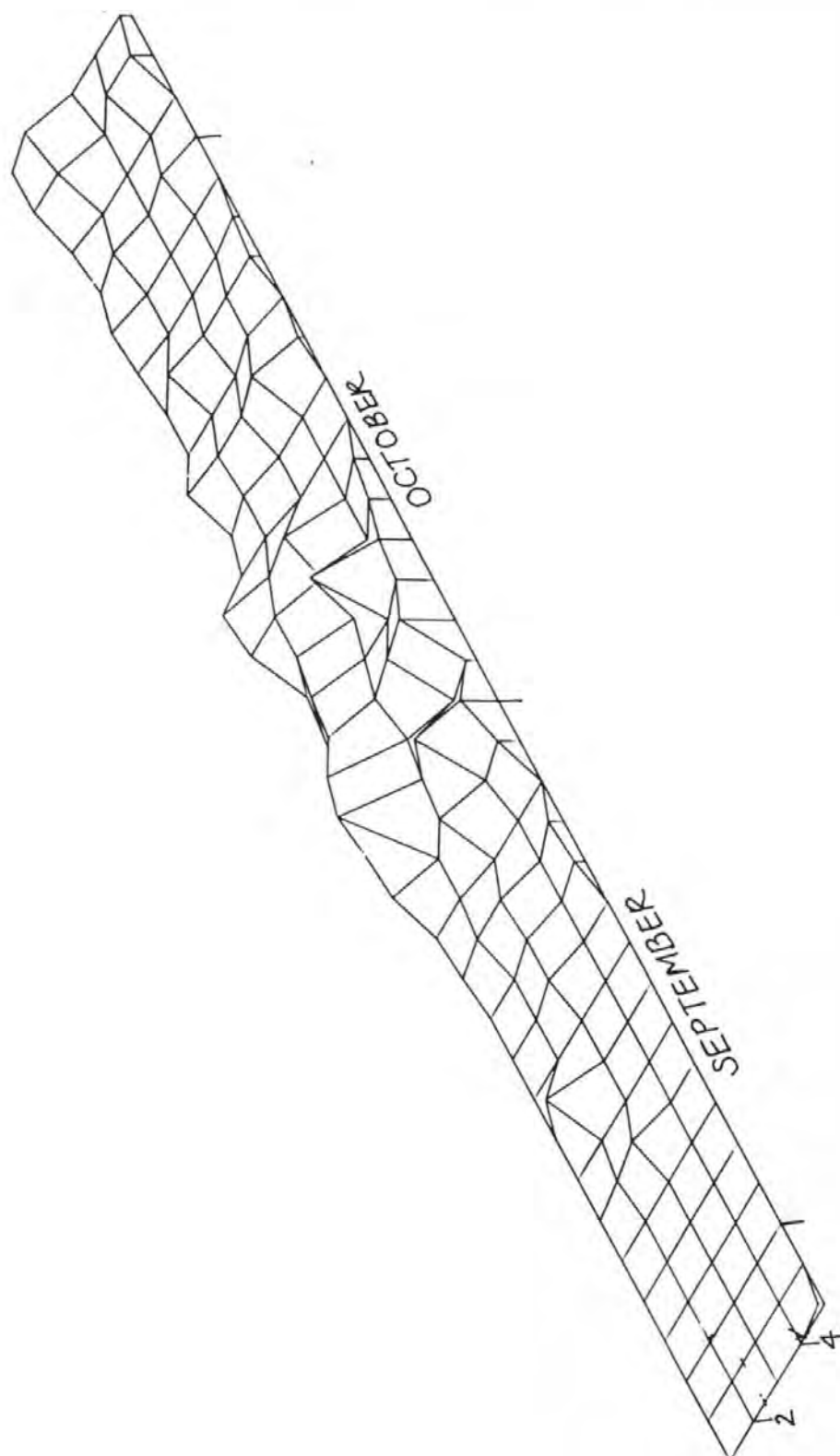
the previous species, this does not reflect the influence of boundaries. The effect of changes in the crop will be discussed in Section 4.6.

There are no significant interaction terms with Date, though again the catches in the gutters continue later than those in the field. Although there is a high mortality of individuals over this period a proportion do over-winter successfully and the field borders provide a better environment than the field (Desender et al 1981). The final significant interaction (Line x Row) is difficult to understand in terms of the heterogeneity in the field and there were no obvious trends in the micro-climate or habitat.

Trechus quadristriatus and Amara aenea: These two species are
treated together as the
Analysis of Variance produces only one significant effect (Date) in either species. Although T. quadristriatus reaches a peak towards the end of October, numbers are fairly constant until a decline in early November. There is a great deal of variation on a day to day basis. In contrast numbers of A. aenea are low after the end of September.

Although as with all species there is a variation between individual traps with neither species are there any significant differences between lines. However it is apparent from Table (4.10) that very few T. quadristriatus were caught in the gutter traps. As these are known to be less effective for small carabids (Luff 1975) this is probably due to trapping efficiency and cannot be interpreted purely as a difference in numbers in the two areas.

The results of the Analysis of Variance from the final site, Rumleigh 1985, are obviously affected by the barrier surrounding the

Table 4.11:

Rumleigh 1985; Individual Trap Totals

4.11a Pterostichus madidus

	G	66	14 Pitfalls		15	G	LINE TOTAL	ROW TOTAL
0m	35	9 7	2	11	14	9	43	1 64
5m		5 2	7	1	5		20	2 66
10m	27	0 2	1	2	5	8	10	3 38
15m		1 2	1	4	7		15	4 55
20m	43	1 5	1	1	13	6	21	5 101
25m		9 7	1	3	2		22	
30m	37	8 3	1	1	6	2	19	
35m		3 1	1	5	6		16	
40m	28	5 5	4	7	4	12	25	
45m		1 7	3	2	4		17	
50m	21	5 5	3	3	15	9	31	
55m	39	17 20	13	15	20	24	85	
	G	39	39		30	G		

4.11b Pterostichus melanarius

	G	121	56		35		LINE TOTAL	ROW TOTAL
0m	137	18 13	13	29	29	16	102	1 193
5m		14 9	18	22	16		79	2 188
10m	191	9 21	9	24	10	8	73	3 180
15m		14 17	10	15	9		65	4 185
20m	221	26 25	15	19	18	14	103	5 203
25m		14 14	10	5	19		62	
30m	168	12 11	22	9	20	12	74	
35m		8 9	13	11	10		51	
40m	204	10 12	10	10	8	10	50	
45m		14 12	11	12	10		59	
50m	110	10 17	18	8	29	12	82	
55m	172	44 28	31	21	25	61	149	
	G	39	39		30	G		

4.11c Pterostichus Cupreus

	G	8		16		9	G	LINE TOTAL	ROW TOTAL
0m	34	32	20	24	23	43	6	142	1 162
5m		10	8	12	8	6		44	2 162
10m	68	3	6	6	4	7	7	26	3 183
15m		15	11	9	4	7		46	4 108
20m	73	12	8	11	9	5	6	45	5 145
25m		12	11	13	4	9		49	
30m	60	12	20	13	5	8	2	58	
35m		14	15	14	12	8		63	
40m	39	15	13	23	6	4	10	61	
45m		13	14	19	5	3		54	
50m	26	9	11	16	9	10	6	55	
55m	35	15	25	23	19	35	15	117	
	G	23		21		10	G		

4.11d Harpalus rufipes

	G	243		107		76	G	LINE TOTAL	ROW TOTAL
0m	175	30	19	8	15	36	18	108	1 194
5m		13	7	5	9	14		48	2 121
10m	165	16	5	2	3	8	22	34	3 85
15m		14	4	4	5	11		38	4 91
20m	176	12	10	7	4	22	18	55	5 221
25m		15	14	1	2	33		65	
30m	99	8	3	4	9	9	19	33	
35m		14	9	5	3	8		39	
40m	113	9	11	4	8	7	26	39	
45m		15	5	4	3	8		35	
50m	36	14	6	7	1	25	6	53	
55m	126	34	28	34	29	40	74	165	
	G	71		56		91	G		

plot preventing emigration and immigration. The four species;
P. cupreus, P. madidus, P. melanarius and H. rufipes, are shown in
Table (4.7d) and the totals of the 60 pitfalls together with the
gutter traps outside the plot (but not used in the analysis) are found
in Tables (4.11a-d).

Pterostichus cupreus: Rumleigh was the only site at which this
species was caught in large numbers. As a
spring breeder large numbers were caught at the end of May and early
June (Fig. 4.16a,b) and the analysis shows that the change in catch is
significant. The barriers had an influence on the distribution of all
species with more being caught in traps adjacent to them. This was
particularly true of the barriers at the top and bottom of the plot
where there was more vegetation. The cabbages were in rows parrallel
to the barriers and hence there was a gap of about 30 cm between the
cabbages and the side barriers, whilst the cabbages touched the
barrier at the top and bottom. The plot was also on a slope and so
there was a tendency for the traps at the bottom to be damper.

These effects are mirrored in the significant Line and Row
factors. Greater numbers are caught at either end of both trapping
dimensions. The results could be due to beetles preferring conditions
adjacent to the barriers or may be due to a mechanical effect of
hitting the polythene (i.e. edge effects). These effects are
investigated in a simulation model in Section 7.

In P. cupreus there is also an interaction between Date x Row
which proves significant and is illustrated in Fig. (4.40). At the
end of May more individuals were found in row #1, whilst there a
follows a trend towards row #5. This type of interaction in the
results at Rumleigh is due to changes in habitat over the summer as

Figure 4.40: Pterostichus cupreus, Rumleigh 1985
Date x Row relationship
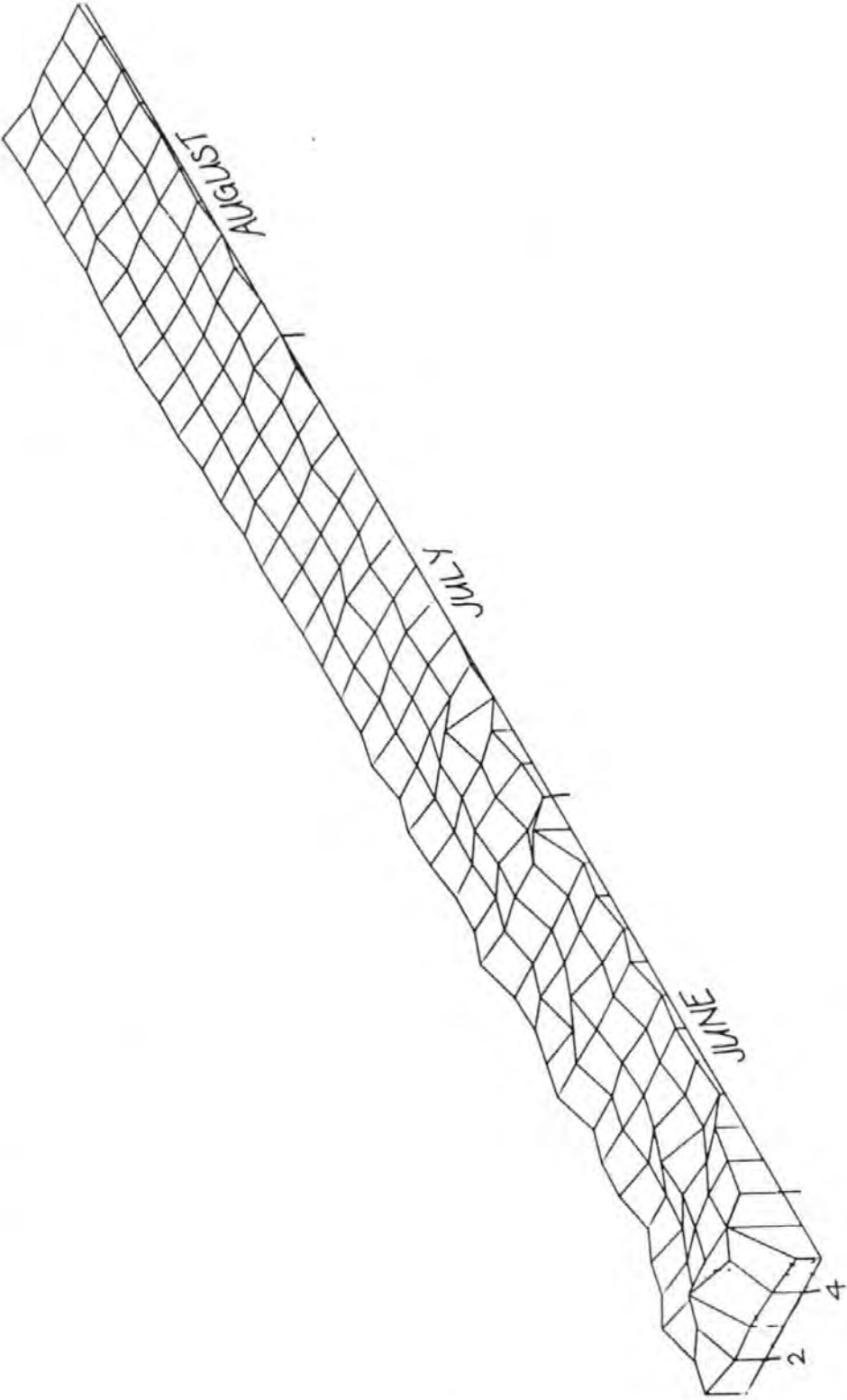
cabbages increased in size and the number of weeds changed. The Line x Row significant factor may be caused by some trend in habitat across the plot, though it is not shown by the other species.

Pterostichus madidus: Fig. (4.17c) shows that this species was caught in low numbers but increased at the begining of August, the change being significant. The results of the Line and Row factors are due to the influences mentioned for P. cupreus, though P. madidus shows a more marked tendency to be caught in the pitfalls at the bottom of the plot. Both Date x Line and Date x Row interactions are significant (Figs. 4.41, 4.42), however the species will be responding to different influences to those on P. cupreus as the main periods of activity are seperated by a number of months.

Pterostichus melanarius: This was the most abundant species in the traps at Rumleigh and shows a different pattern of significant effects in the analysis. The change in numbers caught over the period (Fig. 4.17a) shows that there was a marked increase at the end of May , followed by a reduction in July and a similar increase in late July and August. A variety of species showed a reduction in numbers caught during July and this coincided with a period of very high predation in the traps. However it is considered that predation only caused part of the decrease in number and that there was a reduction in activity and/or density due to the hot,dry weather.

Table (4.11c) and the analysis show that although there were significant differences between the lines of traps caused by the barriers, there was a much smaller effect on the totals on the trap

Figure 4.41: _Pterostichus madidus_, Rumleigh 1985
Date x Line relationship

Figure 4.42: Pterostichus madidus, Rumleigh 1985
Date x Row relationship
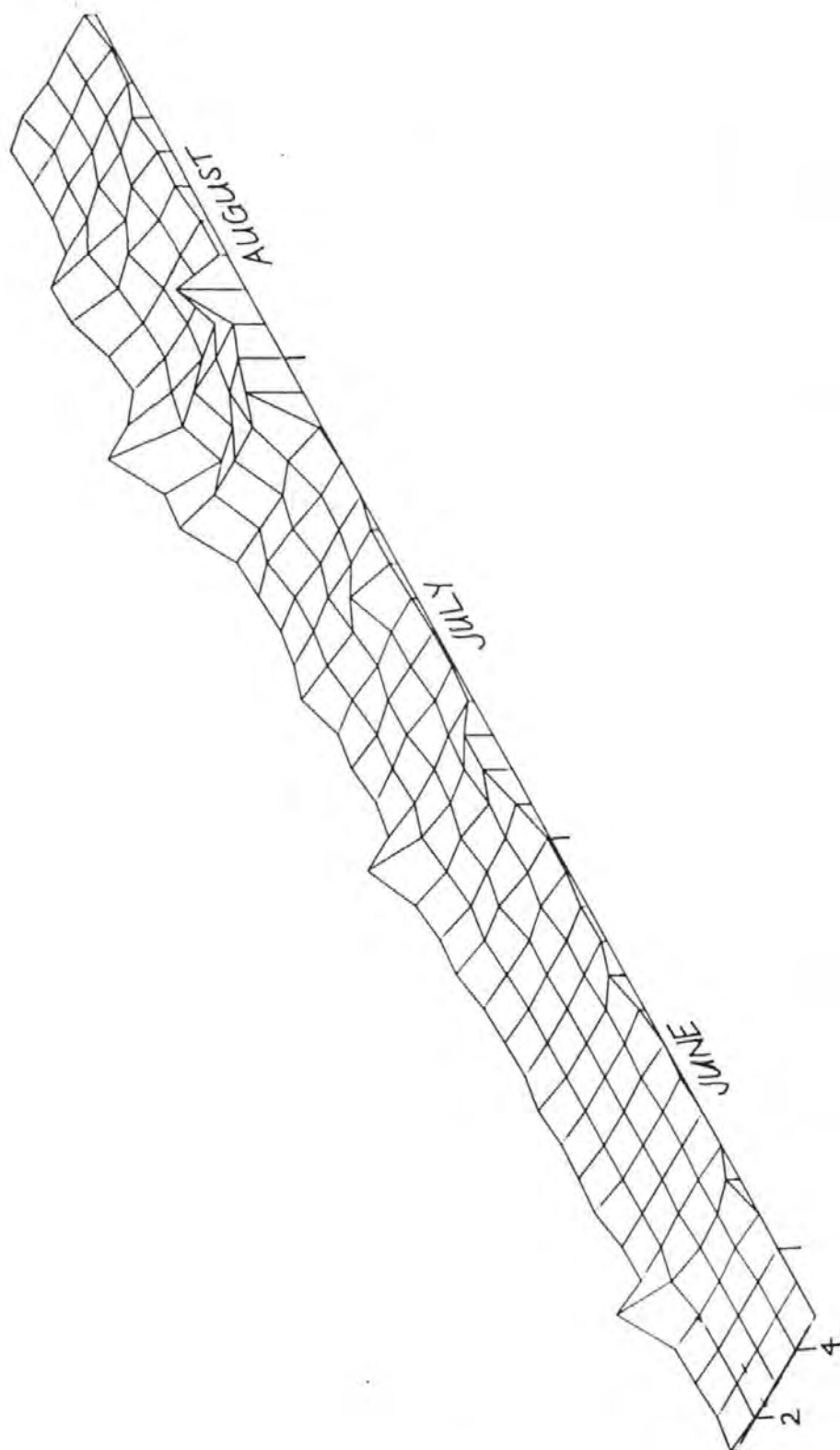
rows. The barriers had less effect on the distribution of this species than on the others, further explored in Section 4.6. The interactions with Date are not significant, however there is a relationship between Line x Row. This is due to the species responding to similar changes in the plot as P. madidus.

Harpalus rufipes: The final species has a similar activity pattern to P. melanarius over the summer (Fig. 4.18a), though there is a less marked peak at the end of June. This was the species most affected by the presence of the barrier and both Line and Row factors are significant. As with the previous species, other than P. cupreus, most were caught in the pitfalls at the bottom of the plot, relatively few were found away from the barrier itself.

Both of the interactions with Date are significant and shown in Figs. (4.43, 4.44) and it would appear to be changing its distribution in the plot in a similar manner to P. madidus.

The results of the tests covered in the previous section serve to confirm statistically some of the differences in distribution which have been mentioned earlier. The variation between traps may have a number of causes. Many of these are due to the influence of nearby hedges or similar field boundaries but others are caused by subtle variation in the crop environment. The possible reasons behind the often large variations between pitfalls within a habitat are the subject of the next section.

Figue 4.44: Harpalus rufipes, Rumleigh 1985
Date x Row relationship
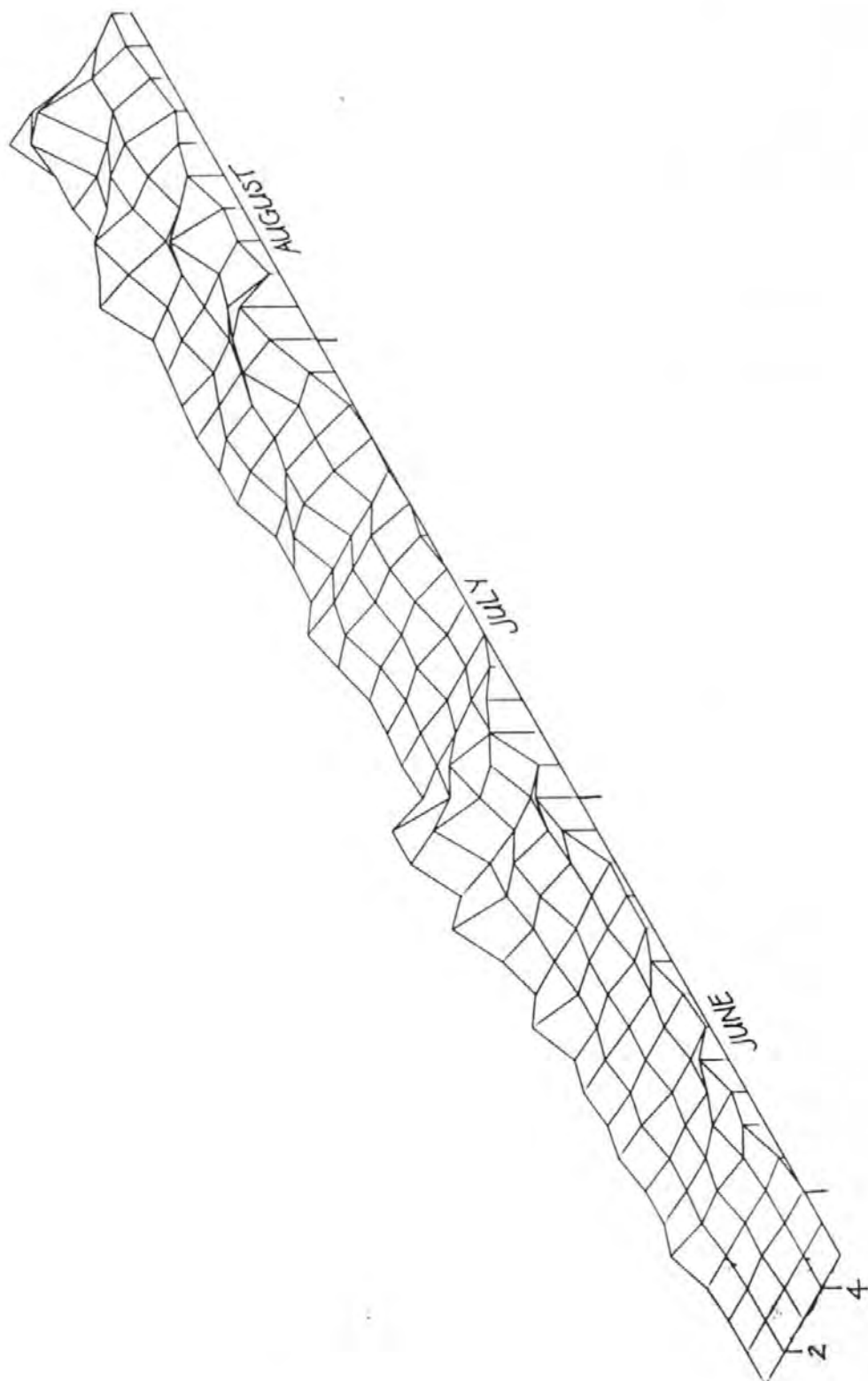
4.6 Variation between Traps

At a number of sites large differences were found between traps which could not be accounted for by the influence of obvious physical features. These could be due to two main factors; variation in carabid density (or activity) or changes in trapping efficiency. The possible patchiness in carabid populations is of primary importance, but alternative causes must be eliminated.

Differences in trapping efficiency can be caused by a number of means (assuming that all traps are identical), for instance if some traps are protruding slightly above the soil surface. These effects can be minimised by maintaining the traps in good condition and reburying them whenever necessary. Keeping a clear area of vegetation around the traps will also reduce the differences. Another cause of variation is if the traps vary in position in relation to the plants themselves. Carabid activity is often concentrated around these (Mitchell 1963b, pers. obs.) and hence during this project all traps were placed in between the rows of plants.

Some indication of whether traps vary due to changes in efficiency can be gained by comparing the numbers of different species caught. Although carabids are likely to have common requirements for certain types of micro-climate, a trap may be suspect if it continually catches large numbers of similar carabids. Similarly if a trap catches very low numbers of all species then it might be suspected that it has a low capture efficiency.

At Staddon Heights in 1985 large differences were found between the catches of different pitfalls, particularly of P. melanarius. There was also a considerable variation in the crop, with some swedes being very small and some areas containing a large number of weeds.

In order to quantify these differences a survey of the area surrounding each pitfall was carried out. The method adopted is outlined below.

Method

An estimate of cover was made using a square quadrat (50 x 50cm) subdivided into 100 5cm squares. This was then placed in an area near to the trap and the number of squares containing brassica leaf, weeds or bare ground recorded. This quadrat was not thrown randomly, rather a patch which was representative of the general area (as judged by eye) was chosen and then the quadrat placed randomly in this area. This was only carried out once at each pitfall and as a further measure the lengths of two swede leaves were recorded at every trap. The results from this survey in Table (4.12).

Results

Although the survey was not intended as as exhaustive sample of the entire site, some interesting results do emerge from the work. The differences between each area can be correlated with the other factors recorded and also with the number of carabids caught in each trap. The results of the correlations are shown in Table (4.13).

Firstly as would be expected the mean leaf length is significantly positively correlated to percentage swede leaf cover and the amount of weeds is negatively related to both. When the swede leaves were small (approx. 20cm in length) they did not form a canopy over the ground, leaving an area where weeds could grow unshaded. As the swede increased in size the weeds were shaded out and the ground

Table 4.12:

Vegetation Index, Staddon Heights 1985

TRAP		%SWEDE	%WEED	%BARE	MEAN LEAF cm.
0m	1	25	47	26	20.5
	2	70	6	11	40.5
	3	95	20	4	51.0
	4	75	30	6	55.5
	5	76	55	5	52.0
10m	1	57	55	7	29.5
	2	83	37	3	45.5
	3	94	17	3	59.5
	4	31	85	3	28.5
	5	83	35	3	43.5
20m	1	61	58	7	36.0
	2	68	70	1	37.5
	3	86	25	1	36.5
	4	92	6	2	55.5
	5	71	64	1	39.0
30m	1	50	38	11	26.0
	2	58	40	5	29.5
	3	35	47	13	29.0
	4	77	45	3	38.0
	5	70	30	14	43.0
40m	1	73	33	1	40.0
	2	84	25	3	50.5
	3	74	49	3	48.0
	4	71	73	6	46.5
	5	87	43	2	41.5
50m	1	54	55	3	36.0
	2	83	40	5	35.5
	3	79	85	0	26.0
	4	43	82	0	38.5
	5	80	60	0	29.5

Table 4.13:

Staddon Heights 1985; Correlation Coefficients

	CROP	WEED	BARE	LEAF	P.mel	C.fus	A.aen	T.qua
WEED	-0.49							
BARE	-0.55	-0.19						
LEAF	0.68	-0.49	-0.33					
P. mel	0.37	-0.31	-0.27	0.43				
C. fus	-1.0	0.04	0.07	-0.11	0.03			
A. aen	-0.14	0.34	-0.27	-0.17	-0.24	0.19		
T. quad	-0.03	-0.19	0.12	-0.01	-0.20	-0.32	-0.15	
N. brev	-0.21	0.20	-0.00	-0.37	-0.36	0.39	0.33	-0.26

___ -Significant, 5% level

often became clear. Apart from this reduction in weed growth

underneath the most luxuriant areas of swedes, there was an increase

in the number of weeds on the south of the pitfall grid (i.e. rows #4

and #5).

Of the carabids P. melanarius is significantly positively

correlated with the amount of swede growth and negatively correlated

with the amount of weeds and bare ground (though not significantly).

The correlation between this species and the amount of swede cover

suggests that the beetle prefers this particular micro-habitat, and

may avoid areas of bare ground. The reduction in areas of high weed

cover is complicated by the possible effects of the weeds on activity,

but there may also be a reduction in numbers in these areas.

N. brevicollis is inversely correlated with the amount of swede

cover and positively with the number of weeds, whilst C. fuscipes

shows the same pattern and these two species are the only ones

significantly positively correlated. These two carabids appear to

have a different habitat preference to P. melanarius and were captured

in greater numbers in areas where there was both a cover of swedes and

an undergrowth of weeds. The greater numbers caught in areas with

weeds (and hence with the highest restriction to movement) suggests

that there is a real difference in density between the areas

(Greenslade 1964a).

The final two species, Amara aenea and T. quadristriatus do not

show a clear pattern since they were caught in lower numbers. However

A. aenea, known to be a seed feeder (Thiele 1977), shows the strongest

positive correlation with weed density and also has a high negative

correlation with the amount of bare ground. T. quadristriatus is

negatively related with all the other species though it might have

been expected to show a pattern similar to P. melanarius as Mitchell

(1963b) demonstrated that it preferred the areas in and around cabbages.

It is possible that these patterns of capture were caused by differences in trapping efficiency as mentioned above. However it is considered that this can be discounted for a number of reasons. Firstly the different carabid species show different patterns and individual traps do not catch large numbers of all the different species. Also there are good correlations between carabid species and the environmental factors within the crop. Finally these differences between pitfalls are consistant over time. Table (4.14) show the individual trap totals for P. melanarius and N. brevicollis over five periods of time at Staddon Heights.

Through much of the period and through the peak of activity, the majority of P. melanarius catches occur in and around the traps in the bottom right hand corner of the grid, where there was the best growth of swedes. This indicates that the beetles were responding to patchiness in the field habitat. Similarly N. brevicollis showed a tendency to be captured in the top left corner of the grid, although there is more variation in this species.

The patchiness in catches from traps was a feature of all the different sites, though it was most consistant at Staddon Heights in 1985. Although variation in the lines of traps was often related to physical features, individual traps changed in the proportion of the catch which they caught. This may have been due to changes in the crop or in the distribution of prey.

Table (4.15) show the numbers of the two species caught in consecutive periods at Staddon Heights in 1984. These show that, unlike Staddon Heights 1985, there was a greater tendency for the traps catching the largest of the catch to move about in the grid of

Table 4.14:

Staddon Heights 1985: Changes in Trapping Distributions in pitfalls

P. melanarius

	Weeks 1-2						Weeks 3-4				
50m	6	5	5	4	9		3	3	8	12	11
40m	8	4	4	3	11		11	4	5	2	6
30m	8	11	14	12	12		9	12	10	14	3
20m	9	15	29	14	17		12	18	12	13	10
10m	18	19	35	14	15		9	10	19	23	22
0m	4	13	30	16	19		4	14	29	15	14

Weeks 5-6						Weeks 7-8				
7	8	4	5	6		6	1	4	2	6
7	1	6	6	17		4	4	2	2	12
3	11	13	6	1		4	1	4	7	8
10	15	12	11	10		4	0	6	7	8
12	7	33	25	28		3	3	8	5	13
1	7	29	17	21		0	10	8	5	9

N. brevicollis

Weeks 3-4						Weeks 5-6				
0	0	1	0	1		0	2	3	4	6
0	0	2	0	0		0	7	1	2	0
0	3	1	0	0		4	9	2	4	3
0	1	0	0	0		2	4	4	2	1
0	0	0	0	0		4	3	1	0	0
0	0	0	0	0		2	3	3	1	5

Weeks 7-8						Weeks 9-10				
3	8	2	4	6		3	0	1	1	3
2	6	1	1	0		0	1	0	2	0
3	3	6	2	3		0	1	0	2	0
1	2	2	0	1		4	1	0	0	0
4	1	0	1	0		3	4	0	4	1
2	1	0	2	2		0	2	1	2	3

Table 4.15:

Staddon Heights 1984: Changes in Trapping Distributions

P. melanarius

Week 1					Week 2				
18	28	21	13	6	42	20	24	27	13
6	17	10	16	7	54	19	22	13	22
14	9	12	11	12	32	24	13	10	17
28	31	18	3	11	19	23	21	15	23
8	11	12	6	17	28	32	30	16	8
6	12	2	5	4	13	20	32	20	15
12	5	4	3	9	2	0	2	4	10

Week 3					Weeks 4-5				
7	3	1	5	2	2	0	1	5	1
14	4	2	1	3	11	4	4	5	0
4	5	7	4	8	8	2	8	1	5
6	4	6	7	9	8	2	2	2	5
8	5	4	7	3	5	4	5	4	7
3	5	6	12	4	13	5	4	2	2

Weeks 6-7					Weeks 8 onwards				
8	1	7	4	5	3	2	4	3	11
3	4	3	4	2	1	3	1	2	7
17	3	2	3	12	2	3	0	1	3
9	7	1	8	10	3	2	2	3	6
10	4	8	5	14	3	4	4	4	4
10	5	3	7	13	5	2	3	5	1
5	2	12	2	6	10	4	12	6	17

N. brevcollis

Weeks 3-5					Weeks 6-8				
1	0	0	7	4	16	15	7	24	6
5	2	1	11	1	45	16	11	35	15
2	5	0	3	1	25	26	11	15	13
5	3	7	4	4	22	16	16	19	14
0	7	3	0	6	20	31	32	12	9
6	2	12	3	8	16	12	8	17	4
4	0	0	0	4	15	21	5	21	9
17	7	11	33	31	17	22	18	22	41

Weeks 9-11					Weeks 12-14				
69	56	23	34	23	38	30	22	15	25
35	39	41	55	30	12	7	15	33	14
47	23	9	61	40	14	6	0	38	25
72	29	25	22	58	21	7	3	16	17
24	39	44	37	44	15	22	24	15	6
41	30	13	76	23	18	9	17	32	13
33	65	61	39	85	42	41	48	35	47
27	83	49	75	40	87	70	19	49	41

pitfalls. At this site although there were differences within the crop these were not as marked as in the subsequent year. It is possible that the carabids were tracking changes in prey density, although it must be remembered that pitfalls measure the activity in the area rather than density alone. The data in Table (4.14) also shows the effect of the hedge and futher support the interpretation on the results of the Analysis of Variance found in Section 4.5.

At Rumleigh differences between traps were largely affected by the presence of the barrier. Table (4.16) shows the various proportions of the total catch found in each of the different areas. The traps are divided into three zones; 1) those adjacent to the barrier (30 traps), 2) Traps 5m from the barrier (22 traps), and 3) traps 10m away (8 traps). From the results it is obvious that the barrier had an overriding influence on the distribution of H. rufipes, P. madidus and possibly B. lampros. For the remaining species more individuals are captured near the barrier but this is probably due to mechanical responses to meeting the barrier, rather than to their prefering the habitat in this area.

During surveys of the plot at night (Section 4.7) large numbers of beetles were found along the base of the barrier, both on the inside and outside. These were counted on the inside of the barrier, every beetle seen whilst walking around the plot being recorded. The results of six separate counts are shown in Table (4.17).

Although by no means an accurate count, the table does give a good idea of the numbers of the large and medium-sized carabids. The vast majority of these were H. rufipes and they were often seen feeding on seeds which had fallen inside the plot from plants on the outside. It is possible that they remained in this area because of the available food, but an additional enticement was the crevice

Table 4.16:

Rumleigh 1985: Catches of Carabids in relation to Barrier

| | Total Catch | % of total | | |
		Barr	5m	10m
Trechus quadristriatus	134	44.1	33.9	22.0
Bembidion lampros	64	57.7	23.1	19.2
Pterostichus cupreus	471	42.7	27.0	30.3
Pterostichus madidus	324	60.0	27.7	12.3
Pterostichus melanarius	738	41.7	31.2	27.1
Harpalus rufipes	507	63.9	21.9	14.2

NOTE- All individuals unmarked

Table 4.17:

Beetles seen at night near barrier

Species	No. seen
Harpalus rufipes	458
Pterostichus melanarius	54
P. cupreus	46
P. madidus	28
Nebria brevicollis	23
Amara spp.	21
Trechus quadristriatus	15

Table 4.18:

Rumleigh 1985: Correlation coefficients

	P. mad	P. mel	P. cup
P. melanarius	0.60		
P. cupreus	0.52	0.39	
H. rufipes	0.76	0.62	0.57

All significant at 5% level

formed by the movement of the barrier in the wind. This provided an
ideal refuge for the beetles and H. rufipes is said to prefer such
areas (Luff pers. comm.). P. melanarius, although more common in the
pitfalls generally, was seen in much lower numbers. The difference in
recapture rates of these two species is discussed in the following
sections

As at Staddon Heights correlation coefficients can be calculated
for the results of each different species in the grid of traps, Table
(4.18). These all prove to be significant and this probably reflects
the overriding effect of the barrier and the lack of any large
differences in micro-habitat within the plot.

The results from this section show that even within a field
carabid density varies within different patches. Thus the
distribution of a population is affected by a number of factors. The
most imortant is, of course, the availability of suitable habitat, but
the field boundaries also have a large effect, especially on spring
breeders. Finally heterogeneity within the crop is important, though
whether carabids respond to this directly or whether it is due to an
indirect effect on prey distribution is uncertain.

4.7 Tests of the efficiency of the traps and marking methods

The results of Luff's (1975) study of different types of trap has been outlined in an earlier section. Although the results of trapping are not used to estimate population numbers directly, the efficiency of the different types of trap used is important, particular with respect to differences between species. Most of the work on these features was carried out at Skardon Place in the summers of 1984/85, however there were also some experiments in constant temperature rooms.

Retaining efficiency of the traps

Method: This was tested simply by placing a known number of marked beetles in the bottom of a trap. These were then left for at least three days, the number remaining after each day being counted, and thus the percent escaping each day could be calculated. Three different size classes of beetle were tested; small (Asaphidion flavipes, B. lampros, T. quadristratus), medium (N. brevicollis, Agonum dorsale) and large (P. melanarius, H. rufipes). The actual number of individuals placed in the traps varied, but was never more than five.

Results and discussion: Table (4.19) summarises the results for each different group of beetles. The number of individuals and time they were left was varied depending on the size class. Thus the data is arranged as the number of beetle days (no. of individuals x no. of days in the traps) for each group. Luff (1975) found that there were no escapes from the traps most similar to the pitfalls used in this project, whilst in gutter traps he found an overall escape rate of 4%/day for medium and large carabids (the escape of small species was

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Table 4.19:

Escape rates from the traps

	Small		Medium		Large	
	Pit	Gutt	Pit	Gutt	Pit	Gutt
Total days in traps	120	120	85	95	150	150
Number of escapes	3	8	0	9	0	1
% escape/day	2.5	6.7	0	9.5	0	0

Table 4.20:

Capture efficiency

	P. mel	H. ruf
Total no. inds. rel.	56	56
Total no. recap's	136	118

very high). However in his survey the escape rate from gutters was estimated from the gutter itself, rather than from the collecting cup as in this study.

The low escape reflects the difficulty in climbing the glass sides of the pitfalls (as long as these are kept clean). In the gutter traps the lip formed by the base of the gutter over the collecting cup prevented escape, although there was some escape by individuals which avoided this. This was especially true of small species, however in the field it was exceptional to find individuals which were caught in the gutter but whichhad not found their way into the cup.

Capture efficiency

This is a measure of the probability of an encounter with the edge of a trap resulting in a capture. Luff (1975) investigated this by releasing carabids into a small arena filled with soil and containing the traps he was investigating. By observation it was possible to estimate how many encounters with the traps ended in capture. However this was carried out at normal room temperature and in daylight. Because of the problems inherent in this approach it was not adopted in this study and the efficiency was not estimated directly, but the relative efficiency was assessed at Skardon Place. Method: Within the plot equal numbers of pitfall and gutter traps were

installed, two or more species of marked beetle were released in equal numbers from the centre. The numbers trapped each day were then recorded over the following weeks. This occurred on a number of occasions in the summers of 1984/85, with a maximum of 40 individuals being released at any one time.

Results and discussion: The results are summarised in Table (4.20) for

P. melanarius and H. rufipes, and includes data for the first 14 days only (so that mortality or escape from the plot is not a large influence). The number of recaptures for each species is very similar. Assuming that the retention efficiency for each species is similar (from previous section), there are a number of other influences on the results. In the subsequent sections it will be shown that the recapture rate of H. rufipes in the field is much lower than that of P. melanarius, but this is not the case at Skardon Place. Because of the relatively high probability of encountering a trap at Skardon Place, any differences in movement patterns between the two species are difficult to detect. Although the actual number of encounters with the traps is unknown, the results do not suggest that the capture efficiency of H. rufipes is lower than that of P. melanarius. If this were the case then activity of the former species would have to be higher in order to produce the same captures, and mark/recapture results suggest that the reverse is the case. Luff (1975) found that the capture efficiency of the two species was very similar.

Effect of marking on survival

It is important that marking should not have an effect on the survival or behaviour of the beetles. The short term behavioural effects are investigated in the section on mark/recapture, but the direct effect on mortatlity was investigated in the lab.

Method: Groups of N. brevicollis were kept in containers filled with soil in constant temperature rooms ($20^{\circ}c$). Individuals were marked and their survival over the following weeks was compared with an equal number of unmarked controls. Beetles marked with the drill were kept mixed in the same containers as the controls, but painted

carabids had to be segregated as the marks were lost, and confusion was possible.

Results and discussion: Of a total of 50 drilled N. brevicollis, 42 survived for more than six weeks, with none dying in the first two weeks. In the control group 38 beetles survived for the same period. Thus there appeared to be no direct effects of drilling on mortality. Those released in the field were kept over-night before release and mortality in this period was negligible. In the field survival was also for long periods, at Skardon Place 16 individuals (drilled) each of H. rufipes and P. melanarius were released, after six weeks 9 H. rufipes and 12 P. melanarius were still present in the plot.

With the painted beetles the marks did not remain for such long periods. In the lab 30 N. brevicollis were painted and all survived for over a week, though many had lost their marks after this period. It is possible that marking with paint made the individuals more likely to be predated, although this is not likely for the drilled specimens.

Overall it seems that marking had little effect on mortality. Escape from the traps was low, especially as the traps were emptied every few days for most of the period. Capture efficiency is much more difficult to quantify. During tracking at night individuals were seen encountering pitfalls on a number of occasions. Although some of these resulted in a capture, often a beetle would succeed in climbing out of the trap, usually by hanging on to the edge with a rear leg. Thus it would seem likely that capture efficiency in the field with the traps used in thus survey is lower than that found by Luff (1975), but that inter-specific differences, particularly between H. rufipes and P. melanarius may not be important.

5.1 Mark and Recapture Experiments

At each site carabids were marked and released. The method of marking has already been described in Section 2.1, at all sites both painted and individually marked beetles were released. The aim of the procedure was to gain information on dispersal rates and directions, but it is also possible to use the recapture data to estimate population densities. On most occasions the mean displacement each day was calculated, by dividing the distance to the trap by days since release. The results are summarised in Table (5.1)

The species marked concentrated on P. melanarius, N. brevicollis and H. rufipes, with the addition of P. cupreus at Rumleigh in 1985 as these were always the most common carabids. The rates of recapture varied between sites, however P. melanarius always had a high recapture rate whilst that of H. rufipes was low. At Rumleigh recapture rates were much higher than elsewhere, because of the barrier and the large number of traps. The results for each different site are presented below.

Battisborough Cross: The mark/recapture experiments at this site were impeded by the disrupted trapping programme but nonetheless some interesting results do emerge. The numbers of each species marked and the percentage recaptured is shown in Table (5.2), whilst the times and place of release and recapture are detailed in Appendix 2.

At the beginning of the trapping period a total of 272 individually marked N. brevicollis were released from the centre of the trap line in which they were caught. It was hoped that this would provide evidence for movement away from the hedge, as was found by

Table 5.1:

Overall Dispersal Estimates

Pterostichus melanarius

		No	M/day	s.e.
Battisborough Cross	1983	52	6.25	0.81
Staddon Heights	1984	126	4.33	0.34
Rumleigh	1985	212	3.30	0.14
Staddon Heights	1985	126	6.03	0.65

Nebria brevicollis

		No	M/day	s.e.
Battisborough Cross	1983	20	2.69	0.56
Staddon Heights	1984	24	4.27	0.86
Staddon Heights	1985	14	4.11	0.93

Pterostichus cupreus

		No	M/day	s.e.
Rumleigh	1985	283	3.01	0.24

Harpalus rufipes

		No	M/day	s.e.
Rumleigh	1985	42	3.28	0.66

Table 5.2:

Release of marked beetles: Battisborough Cross

Nebria brevicollis- Individually marked

Date	FH	CH	C0	C10	C20	C50	TOT	Recap's
19/5			6	14			20	2
24/5	8	1	3	7	7	3	28	5
27/5	23	5	1	3	7		39	2
30/5	17	5	2	6	3	1	34	
2/6	15	3	4	5	4	1	·32	
3/6	23	4	5	13	14	6	65	5
8/6	10	2	1	6	3		22	1
10/6	12		6	5	4	5	32	1
Total	108	20	28	58	42	16	272	
Recap's	3		1	6	4	2		16

Nebria brevicollis- Painted

Date	Place	No. rel.	Recap's
20/9	CH	31	1
	CG	31	4
27/9	CH	40	1
	CG	40	5
2/11	CH	50	6
	CG	50	4
TOTAL		242	21

Pterostichus melanarius- Painted

Date	Place	No. rel.	Recap's
8/8	C10	31	4
12/8	C10	17	3
19/8	C10	42	3
5/9	C10	48	
5/9	C20	46	1
7/9	C10	63	5
8/9	C10	26	4
13/9	C10	50	10
16/9	C10	48	11
20/9	C10	60	4
26/9	C10	60	7
TOTAL		491	52

marking <u>A. dorsale</u> (Pollard 1968). However only 6 individuals were recaptured during the spring period of activity and of these 3 had moved from the field into the hedgebank (2 from 10m away, 1 from 50m away). The other 3 individuals recaptured were all trapped in the line of traps in which they were released, 2 of them immediately after release. Thus the marking produced no evidence for dispersal away from the hedge in this species, but the limited number of recaptures prevents any firm conclusions.

A further 10 individuals from the release of <u>N. brevicollis</u> were recaptured in the autumn between 17/9/83 to 7/11/83. All but one of these was recaptured in the gutter traps around the field edges (the exception being found in the hedge) and the results suggest that the population as a whole is relatively sedentary, a considerable proportion being displaced only a few metres, at least during the spring period of activity.

In the autumn 242 painted <u>N. brevicollis</u> were released, half in the hedge and half at the field edge. Of the 21 recaptures only 1 was in the hedgerow, the rest were in the gutter traps. All of those recaptured after being released in the hedge were found at the field edge. It was hoped that beetles might move into the hedgebank as this was the supposed over-wintering site. As this did not happen it must be assumed that, as the species is active until the end of November and later, movement to over-wintering sites did not occur during the time of the mark and release period. As the beetles were painted the marks would be lost after a few weeks, although one individual was found the following spring, and so movement back to the hedge would not be detected.

During August and September 491 painted <u>P. melanarius</u> were released (Table 5.2), all in the field. The majority of the 41

recaptures were in the gutter traps along the edge of the field although 5 individuals were trapped in the hedgebank itself. The results show that the field population does move to the field edges and into the boundaries themselves. This does not indicate a relationship with the hedgebank, merely that the species is active in the habitat and not restricted to the field.

It is possible to calculate an average displacement per day for both N. brevicollis and P. melanarius using the data from the autumn releases. As shown in Table (5.1) this gives 6.25m/day for P. melanarius and 2.69m/day for N. brevicollis. The data is not directly comparable as the release points for the two species are different, however they do give an indication which may be compared with the results from subsequent sites.

A number of other species were also marked at this site (Table 5.3), though not in sufficient numbers for the recaptures to provide any information. It should be noted however that H. rufipes has a low recapture compared to P. melanarius, though it was released under exactly the same situation.

The following year at Battisborough Cross a further 144 N. brevicollis were individually marked and released in almost equal numbers in Fallow Hedge and Cabbage Hedge (Table 5.3). As with the previous year it was hoped that those released in the hedge would be captured in the gutter traps as they moved into the field. However only three individuals were captured a second time, 2 of these immediately after release and the third was caught at the end of Fallow Hedge, after having moved the length of the hedge. This individual moved over 100m averaging a displacement of approximately 20m/day.

Table 5.3:

Release of marked beetles: Battisborough Cross 1984

Nebria brevicollis- Individually marked

Date	Site	No. rel.	Recap's
23/5	CH	19	
30/5	CH	27	1
6/6	FH	48	2
8/6	FH	20	
8/6	CH	30	
TOTAL		144	3

Pterostichus melanarius- Painted

Date	Site	No. rel.	Recap's
19/6	TR	22	1
28/6	TR	11	3
20/7	C5	25	5
Total		25	9

Other species, both years

Species	No. rel.	Recap's
B. Lampros	59	1
A. dorsale	33	
P. madidus	38	8
H. rufipes	157	5

In the light of the results of the Analysis of Variance (Section 4.5), suggesting movement of at least a proportion of N. brevicollis from the hedgerow to the field, the above results pose some questions. It is possible that all the beetles avoided recapture, although the gutters account for a relatively large proportion of the edge of the boundary (10%). It is probable that the majority, if not all, the individuals marked were recent emergers and Figs. (4.3, 4.9) show that there is a very restricted period of activity for these beetles. It is therefore possible that they enter summer dormancy after very little spring activity and hence their probability of recapture is very low.

A total of 58 painted P. melanarius were released in June and July (Table 5.3). However little further information was gained by the recaptures though the mean daily displacement was 1.32m/day (calculated for the 9 individuals recaptured). Only 25 H. rufipes were released, none were ever seen again.

Staddon Heights: In 1984 P. melanarius and N. brevicollis were again the object of extensive marking studies, both painted and individually marked. Table (5.4) shows the release of painted beetles, of the P. melanarius 26% were recaptured whilst only a single H. rufipes (2.7%) was found again, repeating the pattern found at the previous site.

A total of 230 individually marked P. melanarius were released, and of these 87 (37.8%) were recaptured (Table 5.4). The distribution of recaptures is shown in Table (5.5), the majority occurring in the pitfalls immediately surrounding the release point. There is no evidence for the beetles having a tendency to disperse in any particular direction, though few are captured in the hedge. In

Table 5.4:

Release of marked individuals: Staddon Heights 1984

Pterostichus melanarius- Painted

Date	Place	No. rel.	Recap'd
15/8	7.5m	39	7
20/8	7.5m	38	13
Total		77	20

Pterostichus melanarius- Individually marked

Date	Place	No. rel.	Recap'd
24/8	12.5m	60	28
27/8	12.5m	50	26
29/8	12.5m	40	16
3/9	12.5m	40	12
12/9	12.5m	40	5
Total		230	87

Nebria brevicollis- Individually marked

Date	Place	No. rel.	Recap'd
16/11	12.5m	50	5
19/11	12.5m	50	4
21/11	12.5m	50	1
28/11	12.5m	50	10
7/12	12.5m	50	6
Total		250	26

Table 5.5:

Staddon Heights 1984; Distribution of marked recaptures

Pterostichus melanarius

40m	0	0	0	0	0
35m	0	1	0	0	1
30m	3	2	2	2	0
25m	3	1	4	1	4
20m	2	1	8	1	6
15m	5	7	9	2	7
10m	6	3	8	6	1
5m	4	3	7	12	0
0m	0	1	1	2	0

Nebria brevicollis, 2nd site

40m	0	0	0	0	0
35m	1	0	1	3	0
30m	0	1	1	1	1
25m	0	1	0	1	0
20m	1	1	1	0	1
15m	0	1	1	0	0
10m	0	0	0	1	0
5m	0	0	0	0	0
0m	2	1	0	0	0

comparison with the capture of unmarked beetles (Table 4.9), there is little evidence that released P. melanarius are caught in a similar pattern. However, as was mentioned in a previous section, the level of variation in the crop was low at this site and the pattern of captures variable.

The mean daily displacement for both the painted and individually marked P. melanarius is similar (3.82 m/day and 4.33 m/day respectively) though Table (5.10a) shows that there is some variation between the different releases. The particularly low value (1.62 m/day) for last release may be caused by the fact that these beetles were released after the main peak of activity (on the 12/9/84) (Fig. 4.14). The reduced catch of individuals during this period suggests that the beetles were moving at a lower rate (although mortality may also have reduced the catch) and a reduction in the displacement would be expected.

Of the 230 individuals released 153 were male and 77 female and the results of the two sexes can be seperated in order to identify any differences in behaviour. Table (5.10a) shows that although the proportion recaptured is similar the daily displacement is lower for females than males (2.79 m/day versus 4.83 m/day). The same results were found in subsequent mark/release experiments and are probably caused by lower activity in the female. This results in the females remaining in the trapping grid for a longer period and hence the final result is that similar proportions are recaptured.

With N. brevicollis a total of 250 beetles were individually marked and released. The recapture programme was disrupted by moving the pitfall traps on the 26/11/84, which coincided with the species becoming most active. Thus 150 individuals were released at the first site with a further 100 at the second. Table (5.4) details the

releases and recaptures, showing that there were only 7 recaptures (4.7%) at the first site with 17 recaptures (14%) at the second. In addition 4 individuals were trapped at the second site after having been released at the first.

The mean daily displacement for the species (4.27 m/day) is very close to that of P. melanarius, although there is a lower proportion recaptured. This could suggest that the species has a lower activity but a higher directionality. These differences are explored in the simulation model (Section 7).

The distribution of recaptures (Table 5.5) does not give any indication that there is any orientation in the species' dispersal behaviour and there is no evidence for any movement towards the field boundaries late in the trapping season.

The following season, Staddon Heights 1985, 380 individually marked P. melanarius and 260 individually marked N. brevicollis were released (Table 5.6). This site differed from the previous one as there were gutter traps on two sides of the field which intercepted beetles moving out of the field or along the edge. Of the 126 recaptures of P. melanarius, 53 were in the gutter traps. The release on 2/9/85 was different from the others in that it took place 50m away from the grid of pitfalls, this was to permit recaptures over much longer distance than was possible within the pitfall grid.

Table (5.10a) gives the number of recaptures and the mean distance covered each day. Ignoring the release from outside the grid, there was some variation in the estimates of dispersal. The mean displacement was 6.03 m/day, higher than that of the previous site, and was higher still for those release outside the grid (7.81 m/day). There is no obvious reason for variation between the different releases, though the final release coincided with

Table 5.6:

Released of marked beetles: Staddon Heights 1985

Pterostichus melanarius- Individually marked

Date	Place*	No. rel.	Recap'd
28/8	MID	100	20
30/8	MID	80	14
2/9	TOP	120	18
13/9	MID	80	28
TOTAL		380	87

Nebria brevicollis- Individually marked

Date	Place*	No. rel.	Recap'd
9/10	MID	120	8
14/10	MID	80	5
21/10	MID	60	1
TOTAL		260	14

* Position relative to pitfall grid

Table 5.7:

Staddon Heights 1985: Distribuition of marked recaptures

5.7a Pterostichus melanarius

	G					
50m	8	Ø	Ø	1	Ø	2
40m	5	Ø	Ø	2	3	1
30m	7	Ø	2	5	3	Ø
20m	11	2	5	10	7	2
10m	11	Ø	2	5	6	7
Øm	4	Ø	1	3	1	3
	G	Ø	3	1	1	2

5.7b Nebria brevicollis

	G					
50m	Ø	1	Ø	Ø	Ø	Ø
40m	1	Ø	Ø	Ø	Ø	Ø
30m	1	Ø	Ø	1	Ø	Ø
20m	2	Ø	Ø	Ø	Ø	Ø
10m	Ø	Ø	1	Ø	Ø	Ø
Øm	3	Ø	Ø	Ø	Ø	Ø
	G	3	1	Ø	Ø	Ø

reduced activity and there is a lower displacement during this period.

The sexes show the same pattern as at the previous site, with the females having a lower activity but with a similar proportion recaptured. The difference is emphasized by the fact that females constitute 39.5% of the marked individuals captured in the pitfalls and only 27.3% of those in the gutters, suggesting that the females are dispersing over shorter distances.

Unlike Staddon Heights 1984, there is a pattern in the recaptures of P. melanarius in this year (Table 5.7). As described in Section 4.6 there was a great deal of heterogeneity in the crop and this was reflected in the pitfall results. The recaptures show, apart from the expected increase in the numbers caught in pitfalls adjacent to the release point, that beetles tend to be caught in the same traps that catch large numbers of unmarked individuals. Larger numbers are caught in those traps in the bottom right of the trap grid where the swede cover is most complete. Also greater numbers were caught in the gutter traps adjoining the pasture (7.7/trap) than in those next to the track (1.4/trap). It was suggested that these differences are the result of changes in behaviour in the various areas of the crop, particularly in the bottom left area of the grid and a strip along the pasture to the north where the swede was particularly stunted. Beetles in these areas moved with greater speed and directionality and in addition there is probably a tendency to avoid entering these areas.

Justification from the field for this suggestion is tenuous. However of the beetles recaptured in the North Gutters only two were found in traps #1 and #2 after having moved directly from the release point (i.e. were not caught in another trap and then recaptured a second time). These two beetles had a daily displacement of

13.3 m/day, in comparison there were 14 individuals recaptured under the same circumstances in the equivalent traps (5 and 6) at the other end and these had a displacement of 4.3 m/day. This would indicate that beetles might move more rapidly in the areas of stunted swede seperating traps #1 and #2 from the release point than in the areas of more normal growth elsewhere. The reason for the low catch in the West Gutters would be because of the very luxuriant growth in this area reducing activity.

These factors are all explored in the simulation model.

Turning to N. brevicollis, there were 260 marked and released (Table 5.6). A much greater proportion of these moved to the gutter traps than was found with the previous species, of only 13 recaptures 3 were in the pitfalls and 10 individuals were in the gutters. The recapture rate was only 5% and the daily displacement was 4.11 m/day. The numbers caught were too low to warrant further discussion at this point, the low success rate was probably due to the decrease in activity towards the end of the trapping period (Fig. 4.21).

Rumleigh: The situation at this site was very different as the barrier reduced emigration from the plot, increasing the percentage of recaptures. Three different species were marked and released, P. cupreus, P. melanarius and H. rufipes, these being chosen as they were present in large numbers. All releases occurred in the centre of the plot and are detailed in Tables (5.8). The number of recaptures was affected in particular by a very high mortality in the pitfalls due to dry weather and an unknown number of individuals disappearing during a subsequent period of high predation (Section 3.1). The results for each species are presented below.

P. cupreus was abundant at the beginning of the trapping period

Table 5.8:

Release of marked beetles: Rumleigh 1985

Pterostichus cupreus- Individually marked

Date	Place	No. rel.	Recap'd
28/5	MID	50	37
29/5	MID	60	45
3/6	MID	50	35
5/6	MID	50	41
7/6	MID	20	10
12/6	MID	50	34
TOTAL		280	202

Pterostichus melanarius- Individually Marked

Date	Place	No. rel.	Recap'd
5/6	MID	4	1
12/6	MID	4	4
21/6	MID	24	16
24/6	MID	50	25
10/7	MID	100	45
5/8	MID	50	28
TOTAL		232	119

Harpalus rufipes- Individually marked

Date	Place	No. rel.	Recap'd
3/6	MID	10	1
5/6	MID	36	9
7/6	MID	40	7
26/6	MID	50	7
10/7	MID	50	7
5/8	MID	50	6
TOTAL		236	37

TABLE 5.9:

Rumleigh 1985: Distribution of marked recaptures

Pterostichus cupreus

55m	13	5	8	9	23
50m	2	4	4	3	3
45m	1	2	2	0	0
40m	1	1	3	0	3
35m	9	5	6	2	1
30m	5	5	7	3	3
25m	6	11	10	3	5
20m	5	5	7	3	1
15m	4	6	16	1	3
10m	3	5	3	3	2
5m	4	4	7	2	2
0m	3	11	10	4	7

Correlation of distribution of marked
and unmarked captures :-
Correlation coefficient r = 0.807 *

* significant 0.1% level

Pterostichus melanarius

55m	4	1	2	4	3
50m	1	2	4	3	3
45m	2	7	2	5	3
40m	2	5	1	4	2
35m	4	3	4	6	5
30m	3	4	2	0	4
25m	1	4	5	1	4
20m	2	5	4	3	2
15m	1	5	1	5	1
10m	5	2	5	3	0
5m	2	3	7	1	7
0m	4	11	12	4	5

Correlation coefficient r = 0.377 **

** significant 1% level

and 280 individuals were marked and released (Table 5.8). The recapture rate for this species was very high within the plot (68.6%), but it also had the highest mortality in the pitfalls with 103 individuals being found dead. This mortality was entirely due to capture and dessication and it is unlikely that beetles whichwere not captured suffered a similar fate. A further 15 individuals of the species were caught in the gutter traps after having escaped from the plot.

The distribution of recaptures (Table 5.9) is very similar to the distribution of unmarked P. cupreus caught, with greater numbers being caught alongside the barrier. Suprisingly there is little effect of the central release point and the traps in this area do not catch a significantly greater proportion of the individuals, the 12 traps closest to the 22% of the marked and 15% of the unmarked, (Table 5.9).

Although the barrier has an effect of restricting the movement, the daily displacement is similar to that seen in the field for other species, 3.01 m/day, and this might be expected to be an underestimate of that in a free field population. Males have a slightly higher mean displacement than the females (Table 5.10b), the average time to recapture is lower and also a higher proportion are recaptured. this may suggest that males have a higher level of activity , however the differences are small and further study would be neccessary to substantiate them.

There was also a high recapture rate of P. melanarius (51.3%) with 232 individuals released. There was a much lower mortality in the traps with only 21 beetles being found dead. As in the previous species there was an unknown loss to predators in July, although there was also a reduction in activity in this month and so predation was

probably low.

There is a close correlation between the distribution of marked and unmarked captures (Table 5.9) and little effect of the central release. Of the unmarked population 16% were captured in the 12 central traps, whilst 19% of the marked beetles were found in these traps. The majority of recaptures were in the lower half of the plot, especially in the traps adjacent to the south barrier.

The mean daily displacement is lower than that observed in the field, 3.30 m/day probably due to the effect of the barrier. The differences between the releases , ranging between 1.82 m/day to 5.84 m/day, is due to a variety of interacting factors. The first of these is simply that the last release occurred only four weeks before the cessation of trapping, compared to eight weeks for the release #4. The first recapture of an individual many weeks after release produces a very low mean displacement for that individual and so reduces the mean displacement for the whole release, the effect of this being to increase the mean of the final release relative to the others. However there is also a real difference in activity levels between the first five releases and the sixth as they are seperated by the trough of activity in July. Those released on 10/7/85 were not recaptured at all during the first week and peaked at the end of July, 4 weeks after release and coinciding with the increase in numbers caught in the plot for all species (Fig. 4.17). The effect of this delay is to reduce the mean daily displacement as movement away from the release point is restricted. It is possible that all those caught in the first few weeks after the release on 10/7/85 were removed from the traps by predators, but if this had occurred and activity was normal during this period, then approximately 50% of the individuals would have been lost (the usual proportion caught in the first few weeks after

release). If this was the case then it is extremely unlikely that almost all the remainder could have been caught later in the season (there being 45 recaptures, 45%, in total). Thus although predation was an influence during this period there was also a much greater effect of reduction in activity. The final release on 5/8/85 coincides with the increase in numbers caught (Fig. 4.17), hence a higher daily displacement and a lower time to recapture.

Table (5.10a) also shows that the difference found between males and females in the field was also evident within the plot. If there is a higher level of activity in males then, within the restriction of the barrier, the effect would be an increase in the percentage caught and in the number of times individuals are recaptured. The results show that neither of these occur, the values for both sexes being very similar. This could be due to a number of factors including higher mortality in the males or possibly higher directionality in the males.

The recaptures of the final species, H. rufipes, were much lower than the previous two and few were recaptured more than once (Table 5.8). In previous sections it was noted that that recaptures were also low at the other sites. As with P. cupreus there was a high mortality of those captured, 17 individuals being found dead, all but two of these occurred in early summer and were due to dessication.

The effect of the barrier was extremely marked in this species, with only 6 beetles being recaptured in pitfalls which were not adjacent to the polythene. The tendency to be active in this area is also reflected in the fact that this species had the highest proportion of captures outside the plot, with 4 recaptures (8.3%) in the gutters). This was probably due to beetles escaping through the holes in the polythene, though H. rufipes is an able climber.

Despite the very low recapture rate the mean daily displacement,

3.86 m/day, is the highest of all three species, suggesting a high level of activity. The results for each individual (Appendix 2) show that there was a great deal of variation, in particular those beetles which moved directly to the south barrier of the plot had a much higher daily displacement than the other individuals. If these individuals are disregarded then the daily displacement is only 1.48 m/day (calculated for releases #2,#4 and #5 with 6 beetles omitted). Thus there is an apparent process of H. rufipes moving directly away from the release point to the barrier and then effectively not being available to the pitfalls. The effect of lower activity and restriction to the barrier are tested in the simulation model (Section 7).

Other possible explanations for the much lower recapture rate include beetles escaping from the plot or trap avoidance. Although the gutter traps did catch a number of escapees it does not appear that there was a mass exodus through the barrier. Although the species can fly, the recapture rate of painted beetles, which had effectively sealed elytra, was no higher, (see below). It was shown in a previous section that H. rufipes has a similar trapping efficiency to the other species.

Apart from the individually marked beetles a number of beetles painted with flourescent paint were released. The primary intention of this was to allow them to be easily located at night (Section 6). However the numbers caught in the pitfalls were also recorded, though those recaptured were immediately released and so it is not possible to calculate daily displacement. On 1/7/85 there were 50 painted P. melanarius released, resulting in 34 recaptures of which two were in the gutter traps, a further 107 were released on 14/8/85 with 43

Table 5.10a:

Pterostichus melanarius: Dispersal Estimates

Staddon Heights 1984

Release   Recaptures

	Inds	Inds	%	No	days	M/day	s.e
1	60	28	47	36	7.1	2.94	0.50
2	50	26	52	42	6.2	4.99	0.73
3	40	16	40	20	6.2	3.91	1.90
4	40	12	30	21	3.7	4.68	0.84
5	40	5	13	7	5.4	1.62	0.29
Males	153	60	39	95	4.4	4.83	
Females	77	27	35	31	10.9	2.79	

Staddon Heights 1985

Release   Recaptures

	Inds	Inds	%	No	days	M/day	s.e
1	100	20	20	32	13.2	5.31	1.52
2	80	14	18	28	7.2	7.40	1.53
3	120	18	15	27	16.2	7.81	1.48
4	80	28	35	39	8.9	4.42	0.76
Males	215	51	24	85	10.0	6.75	
Females	165	29	18	41	13.4	4.53	

Rumleigh 1985

Release   Recaptures

	Inds	Inds	%	No	days	M/day	s.e
1	4	1	25	1	36.5	0.62	–
2	4	4	100	7	12.4	4.72	3.11
3	24	16	67	22	13.3	2.89	0.83
4	50	25	50	39	10.8	3.39	0.61
5	100	45	45	91	12.4	1.82	0.17
6	50	28	56	52	6.4	5.84	0.86
Males	132	65	49	120	7.9	3.83	
Females	100	55	55	92	14.7	2.61	

<u>Table 5.10b:</u>

<u>Pterostichus cupreus</u>: Dispersal Estimates

Rumleigh 1985

Release   Recaptures

	Inds	Inds	%	No	days	m/day	s.e
1	50	36	72	50	8.0	4.50	0.77
2	60	44	73	65	10.0	4.35	0.63
3	50	32	64	47	14.2	2.49	0.50
4	50	39	78	52	13.7	1.77	0.26
5	20	10	50	18	12.1	1.35	0.25
6	50	31	62	51	12.2	2.17	0.29
Males	109	79	73	124	11.08	3.28	
Females	171	113	66	159	11.88	2.80	

<u>Harpalus rufipes</u>: Dispersal Estimates

Rumleigh 1985

Release   Recaptures

	Inds	Inds	%	No	days	m/day	s.e
1	10	1	10	1	8.5	2.38	-
2	36	8	22	11	15.1	3.96	1.81
3	40	7	18	8	21.8	1.81	0.36
4	50	8	16	10	6.4	3.33	0.76
5	50	7	14	7	16.0	3.45	2.68
6	50	6	12	6	6.8	3.89	0.99

recaptures before the end of trapping (including another two in the gutters). It was not possible to seperate the releases and so some, though very few, of those captured after the 14/8/85 resulted from the first release. On 9/8/85 107 painted H. rufipes were released of which there were only 9 recaptures, including four which had escaped from the plot.

With regard to the differences found between the two sexes, it should be noted that there is a size difference, with the female usually being the larger. For three species the mean length of males and females was calculated, the distance between the tip of the mandibles and the tip of the elytra being measured. In P. melanarius the mean of the females was 17.5mm (N=50, s.e.=0.10), and the mean length of the males was 16.0mm (N=75, s.e.=0.07). For P. cupreus the values were; females 12.4mm (N=50, s.e.=0.07), males 12.3mm (N=50, s.e.=0.05). Finally in H. rufipes the values were 15.6mm (N=50, s.e.=0.11) and 14.5 (N=58, s.e.=0.08) in the females and males respectively. However the results of the mark/recapture are the reverse of what might be expected owing to size.

From the recapture data it is also possible to test the effect of marking and releasing the carabids. This was done by comparing the time and mean displacement each day to the first and then to subsequent recaptures. This was only possible when there were a large number of recaptures, the results for P. melanarius at a number of sites, and P. cupreus at Rumleigh are detailed in Table (5.11). Greenslade (1964b) suggested that there was an effect on dispersal of mark/release, with an increase in the first few days after release. Thus, if there was a similar effect in this study, a greater

Table 5.11:

Changes in dispersal rates

Pterostichus melanarius- Staddon Heights 1984

	1st Recap.			2nd+ Recap		
Rel	No.	Days	m/day	No.	Days	m/day
1	28	7.7	2.67	8	4.7	3.90
2	26	6.2	4.99	16	2.6	5.27
3	16	6.7	4.44	4	4.5	1.79
4	12	4.1	3.61	9	3.2	6.10
5	5	6.8	1.77	2	1.8	1.25
Total	87	7.2	3.72	39	3.3	4.62

Pterostichus melanarius- Staddon Heights 1985

	1st Recap.			2nd+ Recap		
Rel	No.	Days	m/day	No.	Days	m/day
1	20	15.2	6.77	12	7.9	2.89
2	14	7.0	7.84	14	7.4	6.96
4	28	10.3	4.39	11	5.1	7.07
Total	62	11.2	5.94	37	6.9	5.67

Pterostichus melanarius- Rumleigh 1985

	1st Recap.			2nd+ Recap		
Rel	No.	Days	m/day	No.	Days	m/day
2	4	13.4	1.65	3	11.2	8.81
3	16	15.4	2.31	8	7.6	4.44
4	25	13.5	3.26	14	6.1	3.62
5	45	18.5	1.08	46	6.4	2.54
6	28	7.8	5.26	24	4.7	6.52
Total	118	14.2	2.72	95	6.2	4.10

Pterostichus cupreus- Rumleigh 1985

	1st Recap.			2nd+ Recap		
Rel	No.	Days	m/day	No.	Days	m/day
1	36	6.9	5.69	14	10.7	1.43
2	44	8.7	5.66	21	12.7	1.60
3	32	20.3	2.54	15	9.0	2.39
4	39	13.8	1.81	13	13.3	1.65
5	10	13.7	1.59	8	10.0	1.05
6	31	14.3	2.20	20	9.0	2.12
Total	192	12.48	3.59	91	12.3	1.77

displacement per day, and a lower time to recapture, would be expected to the first recapture, with the effect then subsiding. Although there is some variation between releases the situation with P. melanarius is the reverse of this. At Rumleigh 1985 and Staddon Heights 1984, the mean displacement each day is greater after the first recapture. Also at all sites there time to recapture is approximately 50% lower for the second and subsequent recaptures. The difference found in this study compared to Greenslade (1964b) may be due to the fact that the beetles were released fully fed. If the carabids were not foraging for the first few days after release then displacement would be low for this period.

At Rumleigh P. cupreusdid not show the same pattern, with a lower displacement per day following the first recapture. This may be due to various factors. The first of these is that there may have been some effect of marking and handling, similar to that found by Greenslade. As a species which is active during the day, the fact that release occurred during the period of activity may be important. Finally it should be noted that the difference between the displacements was caused primarily by the very high activity after the first two releases. As activity declined after this short period it is to be expected that this should be reflected in the displacement rates after the first recapture.

In conclusion it would appear that the process of mark/release did not have an effect increasing activity. However the situation is not clear and, as with all the releases, a number of factors must be considered before attempting to compare seperate releases. These include changes in activity over the period, the effect of different release points, the different time-scales for recapture and (between sites) the effect of different trap arrangements.

6.1 Individual tracking at night

At Rumleigh in 1985 further information on the dispersal behaviour of beetles was obtained by tracking individual beetles at night. Despite the large volume of research on carabids there has been relatively little study of them at night under field conditions. The plot at Rumleigh, though surrounded by a barrier, provided a relatively natural system with a large number of individuals of two particular species, P. melanarius and H. rufipes. These species were chosen partly because of their abundance but also because it was hoped to throw further light on the causes of the differences between the two species found during the Mark and Recapture experiments covered in the previous section. Included in the section are a number of photographs to illustrate some of the behaviours observed. These were all taken in the plot at night.

Method

Carabids were located within the plot using a torch with red filters, which has no effect on carabid behaviour (Griffiths et.al. 1985) as they appear to be insentive to the light. These beetles were then followed for a period of two hours (or until they were lost), their position being marked at each two minute interval using a numbered plastic tag which was pushed into the ground. The time intervals were measured using a stopwatch which gave an audible bleep at set time intervals, repeatedly. Disturbance was kept to a minimum by only placing the tags in the ground after the carabid had vacated the position. The crop was such that for most of the time the beetles could be observed directly, but when they disappeared underneath

leaves or stones it was found that it was possible to move the obstruction, check the position of the individual, and gently replace it, leaving the beetle undisturbed.

At the end of the period the tags formed a record of the track covered by the beetle. The bearing and distance of each tag from the previous one was recorded and from this data the distance moved and turn made for each two minute period could be calculated, the track could also be recreated. The step length for each period was simply the distance between subsequent tags whilst the turn was later calculated from the bearing of each tag from the previous one. Turns could range from $0-180^{\circ}$ and those in a clockwise direction were considered to be positive, those in a counter-clockwise direction being negative. If the beetle did not move during the period then the step length was 0cm and the turn had no value, when the beetle moved off then the turn was calculated using the bearing of the last step which had been greater than 0cm.

During the period of tracking activities such as moving, resting or feeding were recorded using a small tape recorder with a lapel microphone and a two hour tape. The two minute intervals were recorded on the tape (via the audible bleep of the stopwatch) and as each tag was put in the ground it's number was called out. Thus the record of the beetles behaviour on the tape could easily be related to the track reproduced from the tags. Other invertebrates seen during the period were noted, especially the marks of any carabids as well as the position of the beetle relative to the barrier or the cabbages. Later the tape was analysed and the length of time involved in each activity measured using a stopwatch.

Tracking usually started a few hours after sunset and as far as possible beetles which were some distance from the barrier were chosen

so that this would have no effect on the movement pattern.

Results and Discussion

Data is presented here for five individuals of each of the two species and although this is a small sample there are distinct differences in behaviour. Each of these carabids was followed for at least an hour, on many occasions individuals were lost after only a short time and the results from some of these are noted later in the section. The usual cause of loss was that the beetles disappeared under leaves and then moved off again without being seen. After a period the obstacle was moved to check the beetle's position, by which time it was impossible to relocate it. Despite the large numbers of beetles seen in the plot it was usually possible to identify the individual being followed and it is unlikely that individuals were confused with others. The full list of step length and turn for each beetle is contained in Appendix 3.

The tape recorder provided extensive information on the activities of the beetles and complimented information on the dispersal pattern. Behaviour which was recorded included the beetle being stationary, moving (and possibly searching), feeding and interacting with other animals. Unlike other studies (Griffiths et.al 1985) it was difficult to categorize individual's behaviour whilst moving. Although there were definite periods of searching behaviour and at times the carabids would run very swiftly these formed two extremes of a continuum. Similarly sometimes there was distinct turning behaviour with the beetle changing direction, often whilst stationary, whilst the majority of changes in direction were caused by obstacles and it was unusual for an individual to move in a straight

line for any distance.

Data from the tape recorder is presented for nine of the individuals, but does not cover the entire time that the beetles were tracked. Obviously little information was obtained whilst the carabids were under cover, but data (and sometimes the beetle) was also lost as the tape was turned over.

The total time of tracking and length of time of taped information for the two species is shown in Table (6.1), together with the overall results. These show that P. melanarius is more active than H. rufipes and also shows greater directionality in its movement. Both species spend a large proportion of their time remaining immobile and it is possible that the greater distance covered by P. melanarius is due to greater time spent moving, rather than walking at higher speeds. Figs. (6.1a, 6.1b) show the frequency of the different size step lengths and angles of turn and these reflect the above statements. H. rufipes spends more of the time stationary or moving only short distances and there is a more marked tendency to turn through angles of greater than 90°. It must be remembered that the data on step size and turn is derived from the position at every two minutes and although this is a fairly close approximation to the track of the individual, it bears little relationship to actual turning behaviour.

There appears to be no tendency to turn in a particular direction, with positive and negative turns occurring in almost equal numbers Table (6.1). Neither does there appear to be any relationship between step length and turn, regression of turn against step length shows that there is not a significant relationship for either species (P. melanarius- r=1.1, NS; H. rufipes- r=1.3, NS). Finally there is no relationship between successive steps and turns in the data, serial

Table 6.1:

Overall results of tracking

	P. mel.	H. ruf.
Total time followed	9hrs 10min	7hrs 46min
Total time of tapes	5hrs 54min	6hrs 26min
Mean track length/hr	7.43m	4.90m
Mean step	0.35m	0.30m
Mean turn	82°	95°
% +ve turns	51	48
% -ve turns	49	52
% of time stationary	74%	87%
% of time moving	26%	13%

Frequency of different step lengths

Frequency of different turns
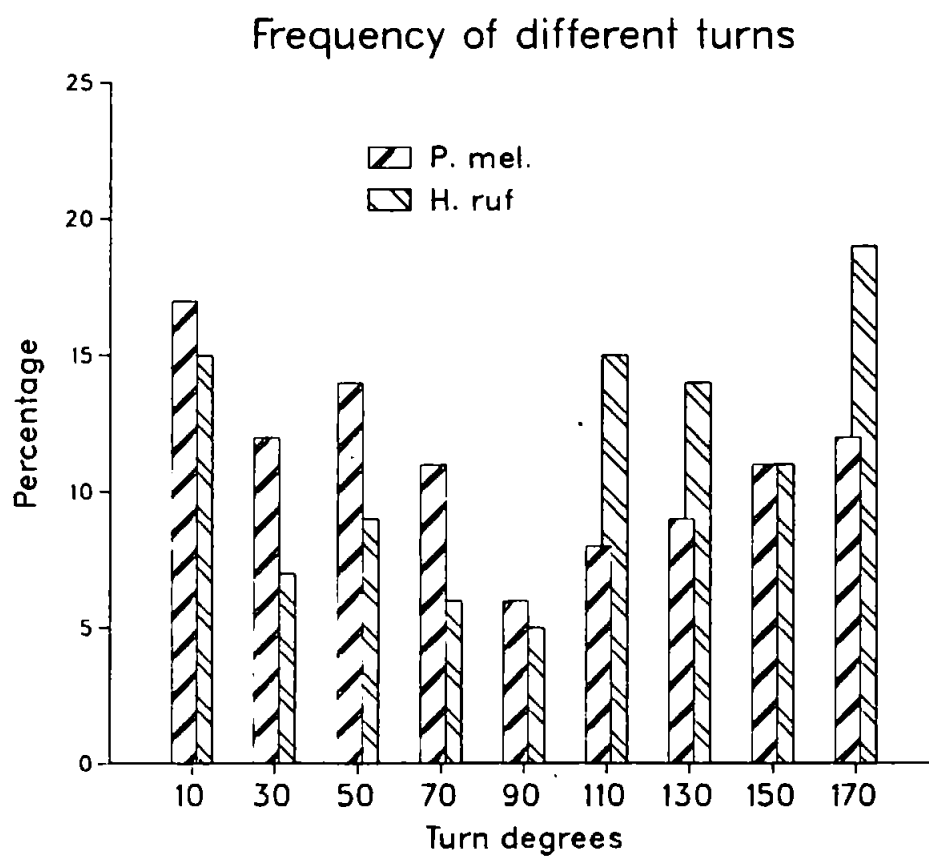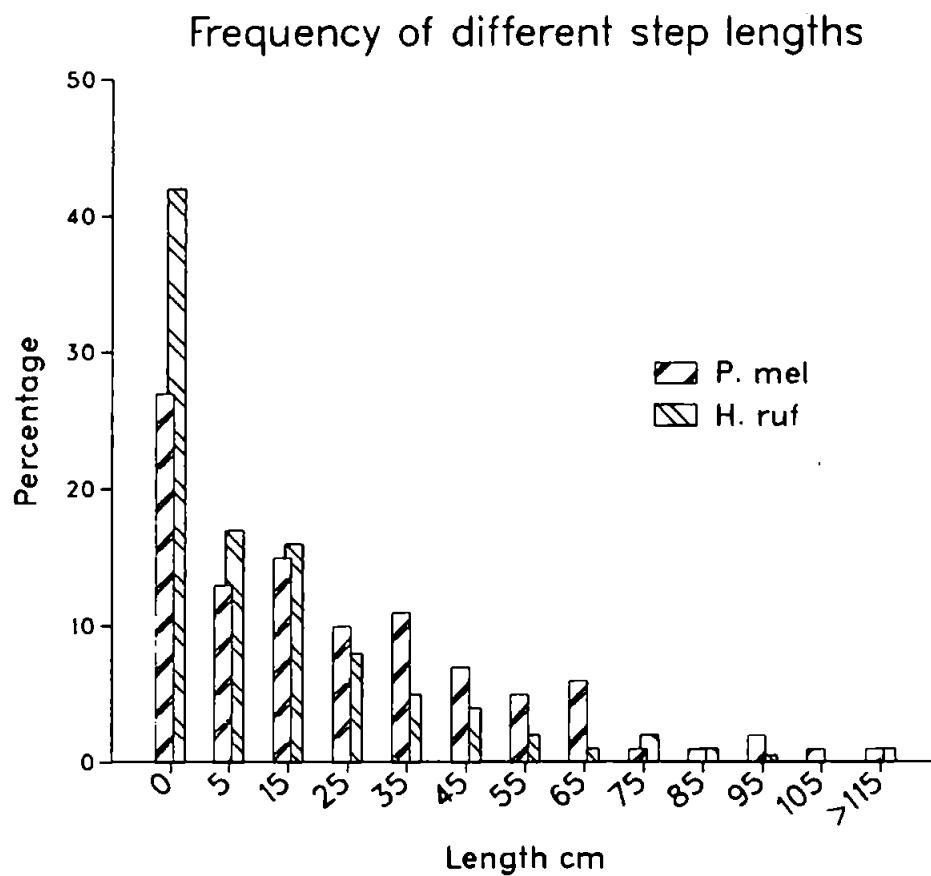
correlation showed that there was no correlation between subsequent movements.

The actual lengths of the periods spent moving or stationary can be measured from the tape and the mean for each species is shown in Table (6.1), with the data for each individual in Appendix 3. For most of the time that the beetles were moving they were likely to have been searching for food items. Although both species moved for short bursts, interrupted by time spent stationary, the data show that P. melanarius foraged for longer periods without stopping. Many of the periods of time for which the beetles were stopped were very short (less than 5s) and these represent interruptions of foraging behaviour during which the beetles stopped perhaps to investigate potential food items or because of obstacles. Longer periods of immobility, 20-30s represent periods when the carabids interrupted foraging in order to clean their antennae and mouthparts. When the beetles stopped for very long periods (the longest being over 25min) for the most part they appeared to be resting and were usually spent under cover. During these times they would groom and were not entirely immobile; they would move about within their refuge, sometimes coming to the edge and then returning back underneath. Fig. (6.2) shows that H. rufipes was more likely to remain inactive for these long periods than P. melanarius.

Turning to each beetle individually there is obviously a great deal of variation in a sample of only five, with one H. rufipes in particular being different from the others (Table 6.2b). There are likely to have been large differences in behaviour owing to hunger levels and perhaps reproductive activities and these are unknown factors. A further complexity is that the tracking was carried on a number of different nights under different environmental conditions.

Table 6.2a:

P. melanarius: Individual results of tracking

Beetle no.	1	2	3	4	5
Track length/hr (m)	10.9	6.2	5.5	7.2	7.5
Mean step (m)	0.40	0.44	0.23	0.33	0.36
Mean turn ($^{\circ}$)	77	77	86	88	85
% time stationary		84	78	75	58
% time moving		16	22	25	42
Mean time stopped (s)		117	55	38	34
mean time moving (s)		24	14	12	25

Table 6.2b:

H. rufipes: Individual results of tracking

Beetle no.	1	2	3	4	5
Track length/hr (m)	4.8	3.6	3.7	9.5	3.0
Mean step (m)	0.24	0.23	0.23	0.53	0.29
Mean turn ($^{\circ}$)	102	94	95	77	107
% time stationary	73	92	91	80	91
% time moving	27	8	9	20	9
Mean time stopped (s)	71	107	110	61	111
Mean time moving	25	10	11	14	11

Lengths of time stopped
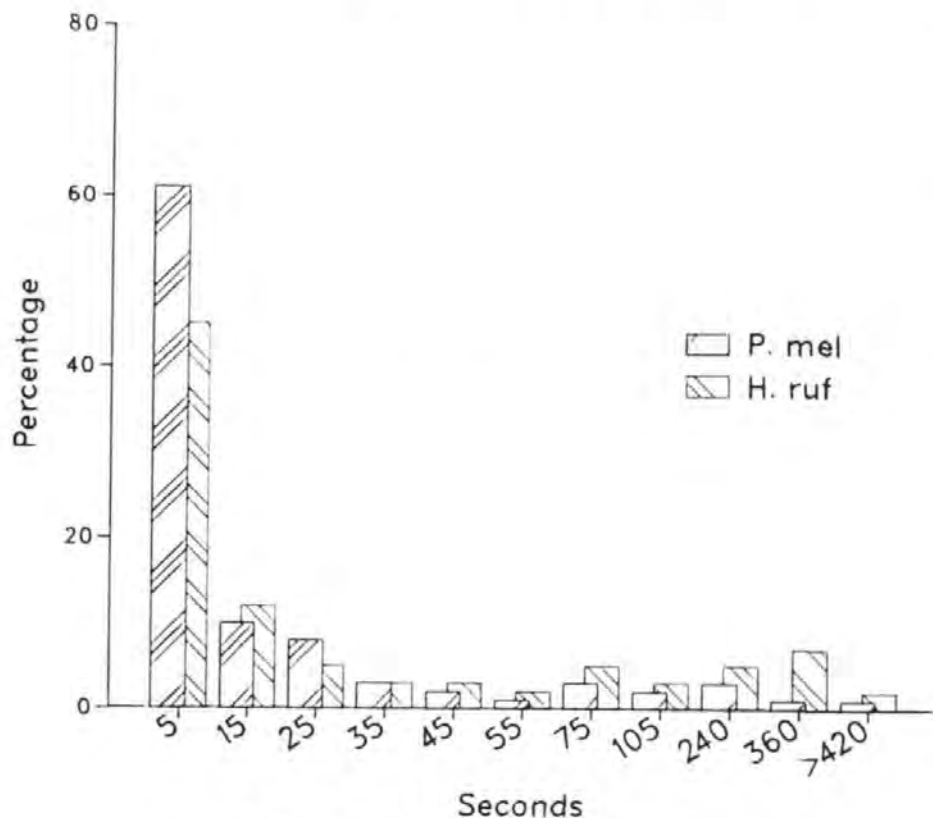
Lengths of time moving
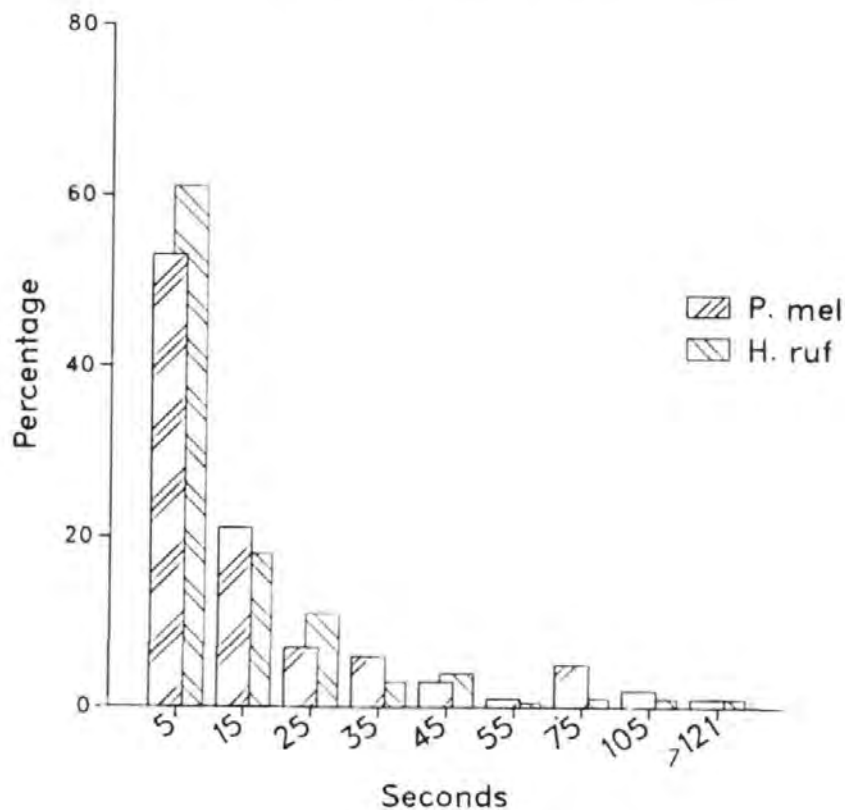
The P. melanarius show less variation than H. rufipes (Table 6.2a), and the different tracks are illustrated in Figs. (6.3a-e, 6.4a-e). The individual with the lowest step length (#3) was the one which was most effected by the presence of the barrier and spent much time foraging amongst a patch of weeds. Although most of the beetles tracked were immobile most of the time, P. melanarius #5 searched almost continuously for much of the period. The same individual was seen again about two hours after tracking had ceased approximately 15m from the position in which it was first found. The tracks of the five H. rufipes are shown in Fig. (6.4), with the individual results in Table (6.2b). Individual #4 had a higher directionality than the other beetles and this may be because it appeared to move more rapidly with little obvious searching.

Broadly speaking it appears that P. melanarius forages in a more wide-ranging pattern, for greater lengths of time. H. rufipes spent more time searching intensively in small areas, turning regularly. All the beetles searched extensively underneath and around the cabbages, but no beetles were seen to actually climb the plants. However at times many H. rufipes individuals (together with Amara spp.) were seen climbing other plants and feeding on seeds, they would also climb the battens holding the polythene in place (Fig. 6.5).

Although not investigated in a quantitative fashion there also appeared to be differences in the foraging techniques of the two species. H. rufipes only searched the soil surface, though the species would push amongst loose soil, whilst P. melanarius was a much more energetic forager, moving small stones and clods of soil as it pushed underneath and amongst them.

Whilst tracking the beetles any prey item found was noted. Three of the H. rufipes found a total of four seeds and consumed them. The

Figure 6.3a,b: Tracks of P. melanarius no.s 1,2

P. melanarius #1

100cm

P. melanarius #2

50cm
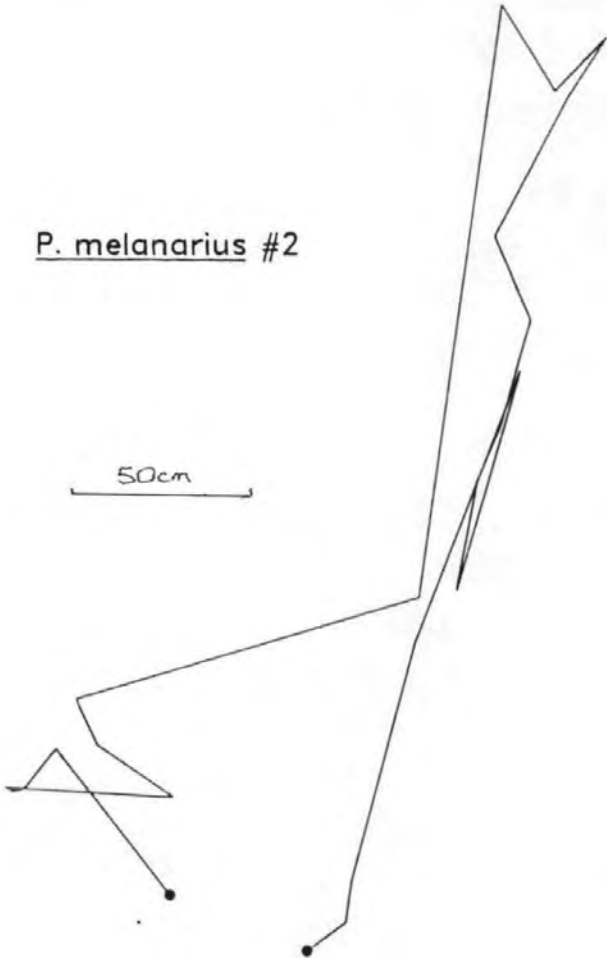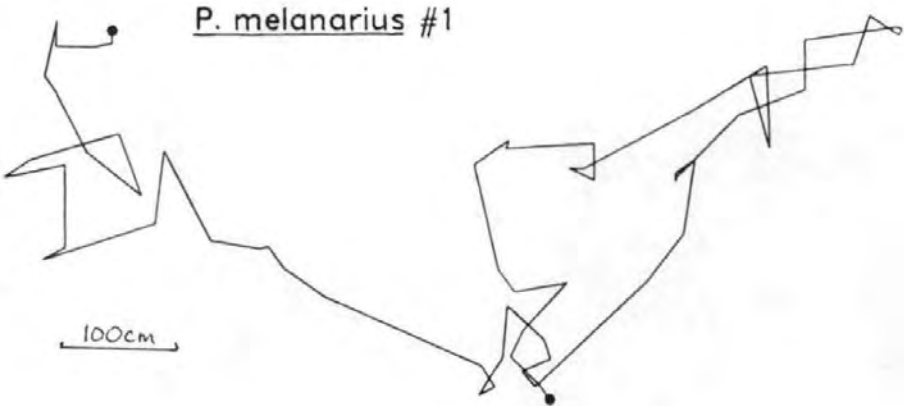
Figure 6.3c,d,e: Tracks of P. melanarius no.s 3,4,5

P. melanarius #3

50cm

P. melanarius #4

50cm

P. melanarius #5

100cm
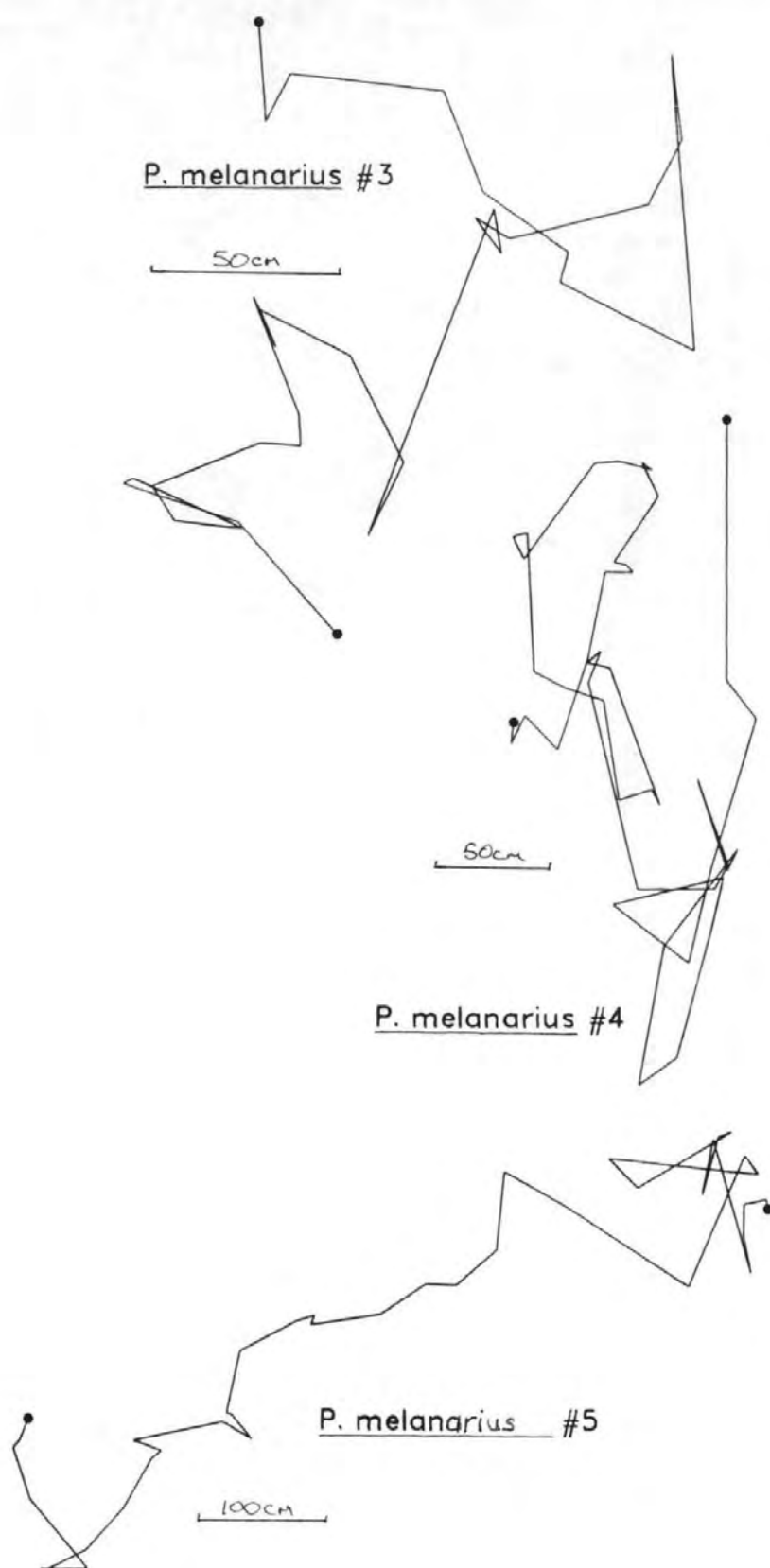
Figure 6.4a,b: Tracks of H. rufipes no.s 1,2

H. rufipes #1

50cm

50cm
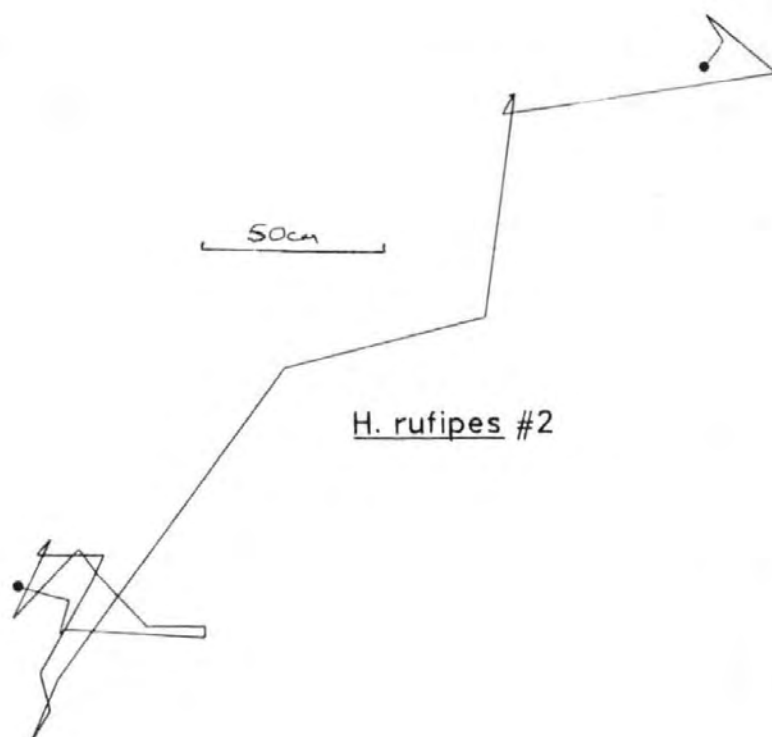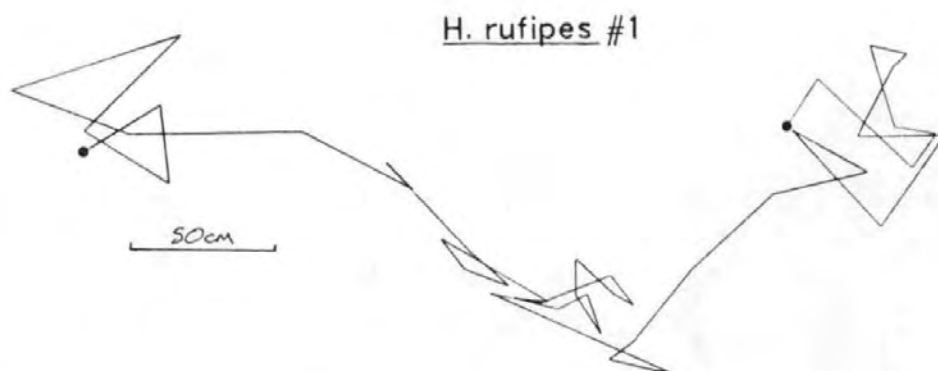
H. rufipes #2

Figure 6.4c,d,e: Tracks of H. rufipes no.s 3,4,5

H. rufipes #3

50cm

H. rufipes #4

50cm

50cm
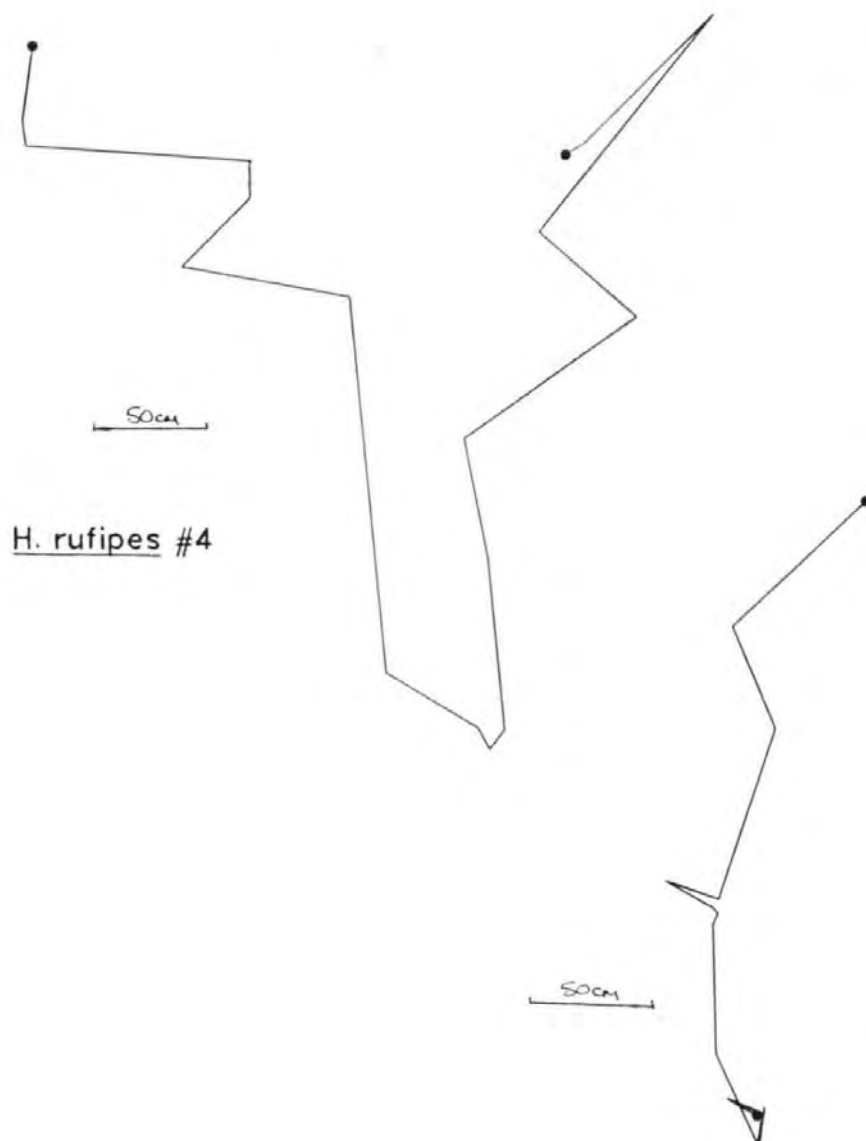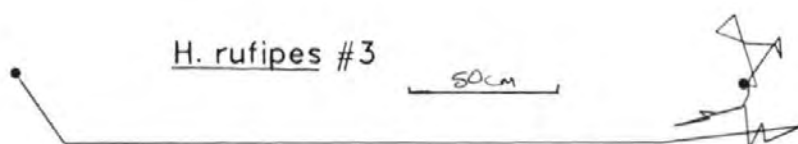
H. rufipes #5

seeds were all compositae (Hieraceum spp) and many other individuals were seen feeding on them close to the barrier (Fig. 6.6). On average feeding on the seeds took approximately 45s, and was followed by area restricted search behaviour during which the beetles often found scraps of the seed. Only one of the P. melanarius found a prey item (a small invertebrate) at the very end of the tracking period. However the beetles would spend long periods of time in cavities in the ground, usually with the head and thorax under the soil. During daylight one of these cavities was excavated and was found to contain a number of large slugs (Arion ater). In the lab carabids of a number of species, including P. melanarius, were seen to feed on the mucus of slugs, both directly from the animal and also from the track left as it moved. Thus it is possible that the beetles were feeding on mucus left in the cavities.

During searches of the plot there were many occasions when carabids were seen feeding. As mentioned above many H. rufipes were seen feeding on seeds, particularly close to the barrier (Fig. 6.6) and P. cupreus and Amara spp. were also seen eating the same seeds. The other main food item appeared to be cutworm (Noctuidae larvae) and again always close to the barrier (Fig. 6.7). Although larger than the carabids themselves both P. melanarius and P. madidus were seen preying on the larvae, other species would then also feed (P. cupreus, H. rufipes and N. brevicollis). It seems likely that only the two larger Pterostichus species were capable of killing the larvae, for the other species it formed a useful source of carrion. A number of individuals would feed at the same time, the most seen was five beetles; 2 P. cupreus, 2 H. rufipes and a single P. madidus. On one occasion a P. madidus was found with a freshly killed cutworm and 1.75 hrs later the above group was found still feeding. Although the

Figure 6.5: <u>H. rufipes</u> climbing a baton

Figure 6.6: <u>H. rufipes</u> feeding on seeds

groups normally seemed to feed with no aggression towards other carabids, on occassion it did lead to competition (Fig. 6.8). No cutworms were ever seen other than those killed by the carabids. Despite the abundance of earthworms in the plot the only carabid found feeding on them was Carabus violaceus. Only a single aphid was found on the ground and this was eaten by a passing P. cupreus.

As mentioned previously all the interactions with other invertebrates seen during tracking were recorded. These were normally with other carabids, particularly near the barrier, though on a number of occasions interactions were noted with Opiliones. The H. rufipes had a total of 20 interactions, usually when two carabids met, and the P. melanarius had 16 interactions. Usually the beetle being followed was stationary and another beetle would run over the top of it. On all the interactions there was a response on only 12 occasions and this usually consisted of moving about 1cm. A response was assumed to have occurred if the beetle moved within a few seconds of being touched. On three occasions beetles which had been resting moved and commenced foraraging after meeting another carabid. None of the interactions appeared to be aggressive and no such behaviour was seen between two carabids at any time.

Thus it appears from the beetles tracked, and a much larger number of other encounters seen between other individuals, that there is little aggression between carabids of the same or different species. Griffiths et.al. (1985) found similar results whilst observing A. dorsale in arenas. Encounters would appear to have little direct effect on dispersal.

Figure 6.7: <u>P. melanarius</u> and <u>N. brevicollis</u> feeding

Figure 6.8: <u>P. melanarius</u> and <u>P. cupreus</u> competing

7.1 Simulation Model

Dispersal behaviour in animals has frequently been explored using stochastic simulation models on computers. These studies have looked at the effects of directionality and activity on spatial distribution and also the inter-relationships between dispersal patterns and food clump distributions (Kitching 1971, Siniff & Jessen 1969, Zalucki & Kitching 1982, Rogers 1977, Jones 1977, Baars 1979). Since in modelling all the assumptions are defined in producing the model, it is possible to test the effects of alternative assumptions (Siniff & Jessen 1969). Computer simulation models are generally not mathematically sophisticated, but simply use the power of computers to cumulate large numbers of simple calculations and relationships. Thus they are based on simple, empirical and testable relationships (Thompson 1979). They are effective in helping to understand the relationships and most useful when producing and analysing non-intuitive results.

It is possible to describe the track of an individual by measuring six components, these are listed by Kitching & Zalucki (1982) as; 1) the mean and 2) the variance of the angle turned through each step, 3) the mean and 4) the variance of the speed of movement, 5) the initial angle of bearing and finally, 6) the proportion of time spent moving. Further complexities can be added these include relationships between step length and angle turned or between successive steps, and and also orientation towards specific areas (e.g. food clumps)

The model used in this study was based on the results of tracking individual beetles at night (Section 6). The data was used to produce frequency distributions of step length and turn which could be used to produce a track. As the results from the tracking were based on the

individual's position every two minutes the model reproduces this. It does not attempt to simulate each actual step of the beetles. Rather than using a theoretical distribution for the frequencies (such as the circular normal) for the turns and step lengths, the observed frequencies are used (c.f. Zalucki & Kitching 1982).

The model is written in Fortran 77 and is detailed in Appendix 4. Random numbers were generated using NAG routines. A flow chart is shown in Fig. 7.1. As with most simulation models the position of an individual was recorded using (x,y) co-ordinates, after each step the new position was calculated using:

$$x_{i+1} = x_i + d(\cos A)$$
$$y_{i+1} = y_i + d(\sin A)$$

where d is the distance moved and A is the bearing. All distances were measured is centimetres and turns in radians.

Between the defined limits (0-180° for turns and approximately 0-200cm for step length) values for turns and step length were continuous and calculated to a high level accuracy. Because of the results of the night tracking it was assumed that clockwise and counter-clockwise turns were equally probable and that there was no relationship between step length and turn, or between successive movements.

In order to compare the results of the simulation model with field data, traps were incorporated into the program. These included both pitfall and gutter traps, the pitfalls were assumed to have a diameter of 9cm, and the gutters were 100cm long, 11cm wide. These are the same dimensions of the traps actually used. Any individual whose track crossed one of these traps then had a certain probability

Figure 7.1; Simulation model flow diagram
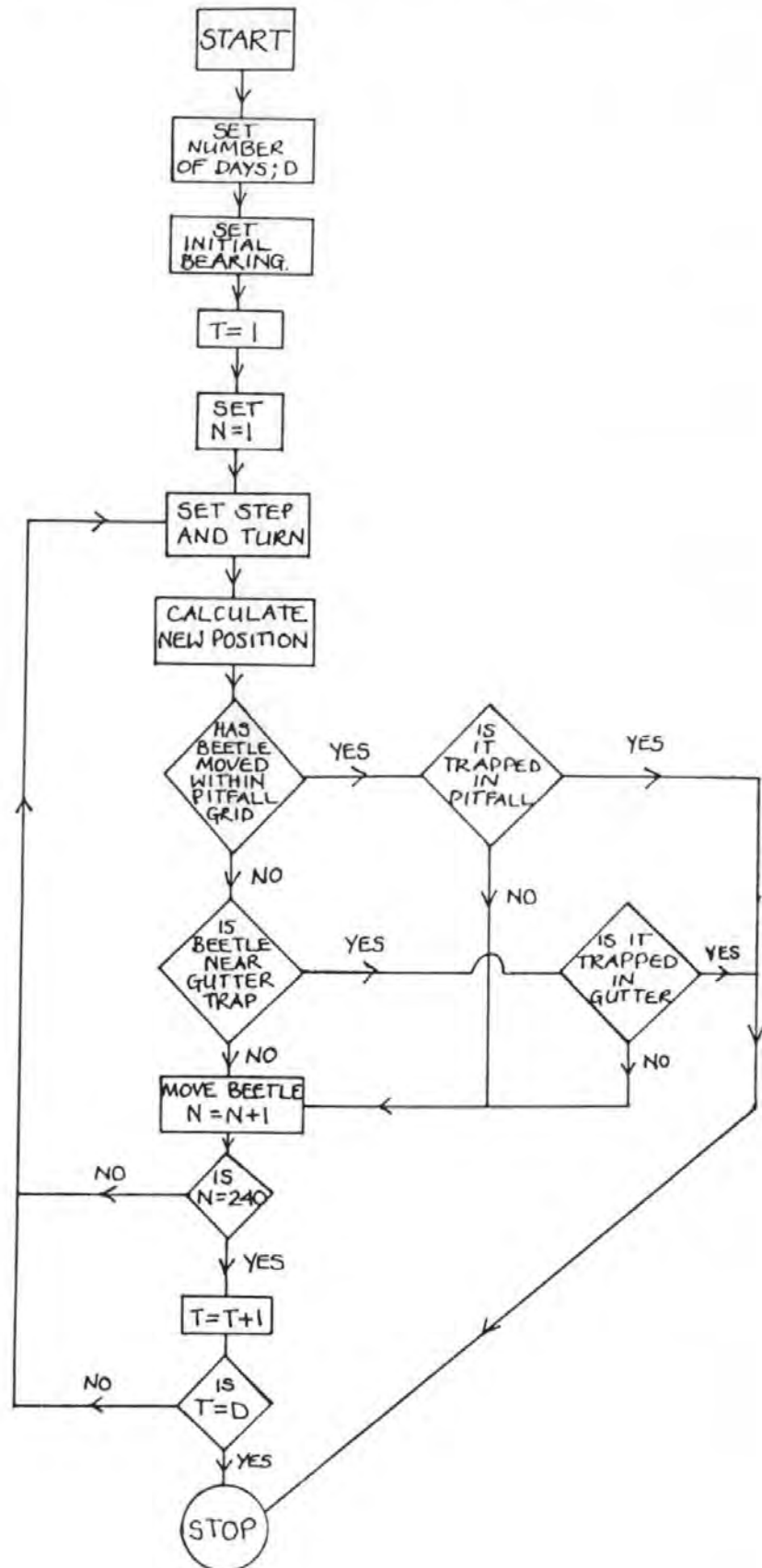
of being captured. If it was not captured then it continued on its way, with no change in behaviour. Pitfalls were arranged in a regular grid and gutters around the edge of this area. Their positions were defined at the beginning of the program.

The pattern of recaptures in the traps, together with the proportion recaptured and the mean displacement each day, allowed the results from the simulations to be compared to the mark/recapture experiments. In the model once a beetle was caught it was removed, multiple recaptures not being possible. As in the field simulated beetles were released from the centre of a grid of pitfalls and the model was then run for a length of time usually corresponding to a number of weeks. It was assumed that activity occurred over an 8hr period each day thus, with the beetle's position every two minutes being calculated, a model day consisted of 240 steps.

Evolution of the model

In this section a brief survey is given of the results of various editions of the model, and the reasons behind its development. Details of the results and discussion is contained in following sections. The initial intention was to use the results from individual tracking to simulate mark/recapture experiments and to determine numbers captured and displacement rates, for comparison with the field data. Changes in activity patterns (rate of movement and directionality) could then be used to investigate differences between species. The first editions of the model were used to do this.

However the results from Staddon Heights 1985 showed that there was patchiness in the results from the pitfalls, possibly reflecting differences in activity or density in different areas of the field.

The results of the vegetation survey were thus incorporated into the simulations producing a patchy system. These patches were assumed to be a 10m square with the pitfall in the centre, each was given an index ranging from 1 to 5 according to the vegetaton. In each different type of patch there were changes in dispersal behaviour.

The model showed that simple changes in activity or directionality in patches could not produce large differences in catch. Reduction in movement could cause changes in density, but because catch is related to activity, there was little variation in total caught. Thus additional factors were included. The first of these allowed delay effects, so that changes in dispersal behaviour did not occur at the boundary between patches. The model was also adapted to resemble the effects of restricted search; the beetles moved in the same pattern throughout the grid, but in different patches there was a varying probability of meeting a prey item and entering a phase of random turn/short step movement. Finally an edition was produced in which individuals could orientate towards favoured areas and thus actively move into them.

All simulations of Staddon Heights occurred in an effectively infinite area, with nothing preventing the beetles moving away from the grid of pitfalls. In alternate models of Rumleigh 1985 the barrier was simulated and beetles were not allowed to move beyond this. Behaviour upon encountering the barrier could be varied. To test the various effects in the model simplified systems were created. These consisted either of homogenous areas without patches, or systems which contained only two different types of patch in a chess-board type arrangement.

Apart from testing the effects of various types of dispersal, the model was also used to test the effect of different trap spacings on

dispersal estimates and the accuracy of these estimates. Finally the effect of step length and directionality on numbers caught in pitfalls was investigated. A more complete presentation of the results and discussion is continued in the next section.

Generation of step length and size

From night tracking of carabids (Section 6) frequency distributions of different step and turn sizes was produced. In order to simplify the model five different size classes for both step and turn were produced. The limits for these were chosen as the tracking suggested that there was an equal probability of any value occurring, within each class. The limits for step length were; 0cm, 1-20cm, 21-40cm, 41-70cm and 71-150cm. Whilst for turn size the limits were; $0-20^{\circ}$, $21-40^{\circ}$, $41-120^{\circ}$, $121-140^{\circ}$ and $141-180^{\circ}$. The frequency distributions associated with these classes are shown in Fig. (7.3). The standard distribution is that of patch-type 3, which is derived from tracking of P. melanarius. The other distributions were created in order to allow changes in movement in the different patches of the Staddon Heights 1985 model.

Changes in movement patterns were produced by altering the frequency distributions rather than by changing the limits. This approach was adopted as it allowed flexibility, yet kept movement within limits which were known to be realistic.

Model Results and Discussion

In order to compare the results of the different models the total amount of activity and numbers of beetles is measured in

Relationship between parameters and catch
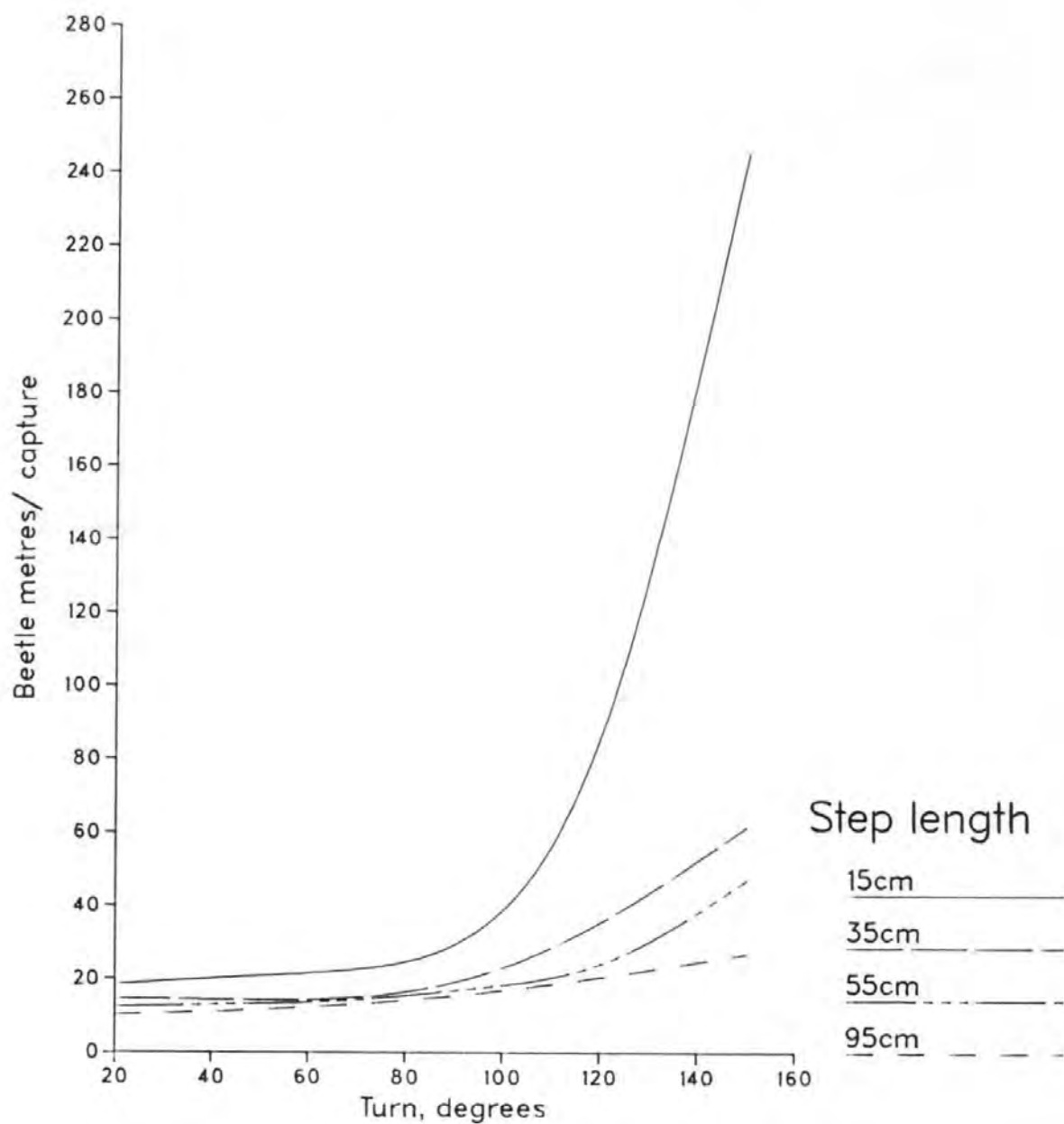
beetle-metres. This is the product of the mean step length and the number of beetles in the area, on most occasions the mean total beetle-metres in a square metre is calculated (Bmm^{-2}).

Relationship between step length, turn and catch

As has been emphasized throughout this work, the numbers of beetle caught in pitfalls is related to the total distance covered on the ground. However there is an additional factor in that the probability of being captured, whilst covering a given distance, is also related to the directionality of the movement. At one extreme when the turn at each step is 0°, and the beetle is moving in a straight line, a new area of ground is searched at each step, with the same chance of encountering a trap. As the turn increases then the probability of covering ground which has already been searched increases. When the turn is 180° then the individual covers the same track continuously, with no chance of being captured after the first step. Between these extremes there is a relationship between mean turn and probability of capture.

The effect of this is that, in order to catch an individual, a greater distance has to be covered by an individual moving with low directionality than one moving directionally. The step length and size of the trap also affect the relationship. Although there is likely to be a mathematical solution to the relationship, the simulation model can be used to explore its nature.

Method

The model was adapted so that the beetles were active in an arena

Frequency of different step classes

Step lengths
- 71–150cm
- 41–70cm
- 21–40cm
- 1–20cm
- 0cm
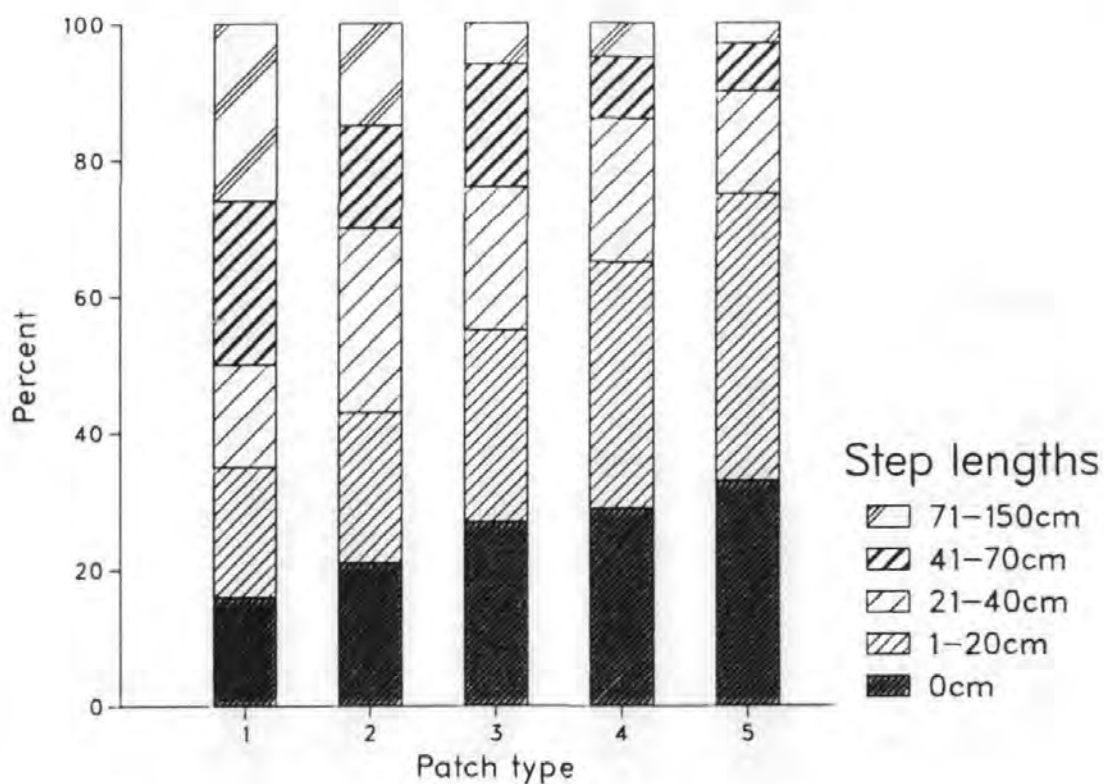
Frequency of different turn classes

Turn size
- 141–180
- 121–140
- 41–120
- 21–40
- 0–20
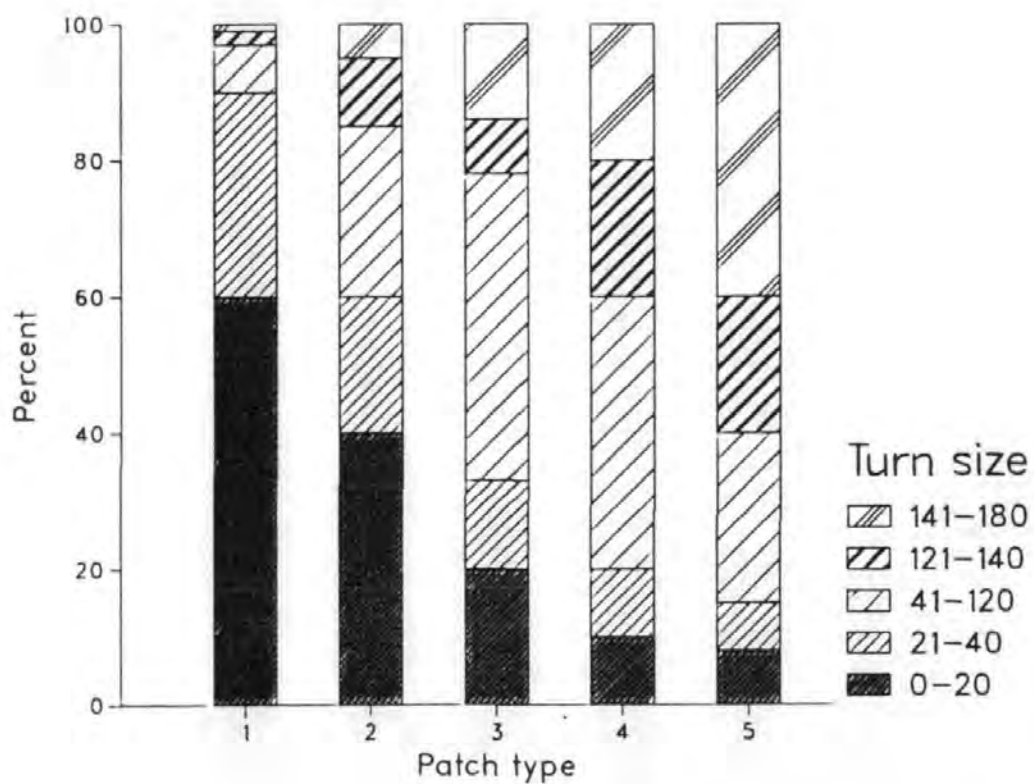
of thirty pitfalls (50m x 40m). The parameters of movement were
fixed, with none of the random variation possible in the other
simulations. The initial position and orientation of each individual
within the arena was chosen at random, and any beetle which moved
beyond the edges of the area was repositioned randomly back within it.

The step lengths chosen were 15cm, 55cm and 95cm, with turns of
20°, 45°, 70°, 95°, and 150°. For each of the 18 different
combinations there were at least three runs of the model, each of 100
beetles for 10 days (a maximum of 240,000 steps). For each run the
number of beetle metres needed to catch an individual was calculated.
To do this the total number of steps and step length was known, and
hence the average number of beetle metres in each square metre. With
30 traps there were thus 30 estimates of the catch produced by this
level of activity. For some combinations more than three runs of the
model were neccessary, this was because at high turns and low step
length there was a very low chance of a capture.

Results and discussion

The results are shown in Fig. (7.2) and it can be seen that the
catch is inversely related to turn and positively related to step
length. At the two extremes the curves for each step length should
meet, the number caught when the turn is 180° being related to the
initial position. At 0° the number of beetle-metres required to catch
an individual is approximatley 10bmm^{-2}, between these two limits the
curves diverge.

These curves are calculated for a trap diameter of 9cm and the
relationships would change for different area traps. For smaller
traps the curves would effectively be flattened, the 95cm curve

becoming similar to the 15cm curve. This is because the probability of covering the same area is reduced, and so the curves become more alike, though the distance covered to produce a catch is increased. Conversely for larger traps, the 95cm curve would attain a shape similar to the 15cm curve in Fig. (7.2). This is because there is a higher probability of searching the same area more than once.

The results show the effects of step length and turn on the numbers caught in traps. If other factors are equal then beetles with low step length and high turn rate will be caught in much lower numbers than those with longer steps moving directionally. These relationships should be remembered when considering the following sections, which investigate the possibilities of using the data from the frequency distributions of step length and turn to simulate the results of mark/recapture experiments.

The simulation in the field

In Section 5 the results of calculations of the daily displacement is shown for a number of sites and species. The first aim of the simulation model was to see whether the estimates derived from night tracking at Rumleigh could generate what might be happening in the field. The frequency distributions used in the model for P. melanarius are shown in Fig. (7.3, patch-type 3), it can be seen that 5 different step lengths and turns were used, with associated probabilities.

Method

In order to test the results from using the above frequency

distributions the model was set up so that it had the same pattern of traps as Staddon Heights 1984. Thus there were 40 traps in 8 lines of 5 traps, the lines being 5m apart and the traps 10m apart within the lines. The beetles were released from the same point as those in the field (near the centre of the grid), and each simulation consisted of 150 individuals moving for 3 weeks. There was no limit to their movements, the arena being of infinite size.

Results and discussion

At the end of the simulation the daily displacement of each of the trapped beetles was known, as was the days to capture. The mean displacement after three runs of the model was 3.21m/day, time to capture being 7.15 days. Although slightly lower than the field results (Table 5.10, disp=4.33m/day, time=5.72) the model produces similar values. This suggested that use of the results from Rumleigh was at least a good approximation to the situation in the field, although it would appear that directionality and activity may have been higher in the population at Staddon Heights.

At this point no further simulations along this line were made, instead attention was transferred to Staddon Heights 1985. As has been shown in previous sections there was a great deal of variation in the catches. The model was altered so as to include the differences in the crop, with the 30 different 10m squares making up the trapping area being given an index from 1 to 5. The arrangement of the patches is shown in Table (7.1) and is taken directly from the results of the vegetation survey at the site.

The changes in dispersal behaviour in the different patches were

Table 6.1:

Distribution of vegetation index, Staddon Heights 1985

```
50m  2  4  2  1  3
40m  4  5  3  2  4
30m  3  3  1  4  4
20m  2  2  5  5  2
10m  2  4  5  1  1
 0m  1  5  5  4  3
```

1- Small swedes, sparsely distributed, much bare ground
2- Small swedes, many weeds
3- Medium swedes, little bare ground
4- Large swedes
5- Very large swedes, few weeds

Outside grid, all areas had an index of 3, except area between row #1 and gutters. This had an index of 1.

made by altering the frequency distributions of the steps and turns. Five different sets of frequencies were produced, which are detailed in Fig. (7.3), these were chosen after trying a variety of different possibilities. The method adopted for producing the various levels of dispersal maintained the basic results from night tracking, but provided the possibility for the beetles to increase or decrease dispersal rates in the different patches. The effect is that in patches with a value of 1 the beetles moved rapidly with a high directionality, whilst in patch-type 5 they moved with a shorter mean step and low directionality.

At first the simulations were carried out in the complete Staddon Heights 1985 model, with 5 different patches and gutter traps. However because of the complexity of the results a simpler model was produced in order to test the effects of the various changes which were made. This consisted of the 30 traps arranged in the same pattern, however only two types of patch were used (normally types 1 and 5), arranged in a chess-board pattern.

The aim of the simulations was to find some combinination of parameters which would allow an increase in the catch in certain parts of the arena.

Method

A number of different types of movement were simulated using this model. In order to identify trends in the results more quickly, extremes of movement were used, i.e. patch-types 1 and 5, although if one of the parameters was kept constant then a mid-range value was used. Each simulation run consisted of 150 beetles over 3 weeks, although as there was no limit on the arena, the number of steps

within the trapping area varied greatly. The number of runs changed according to the scenario and the results of each run were averaged. However the results of the runs were very consistent, each produced from a minimum of several hundred thousand steps in the grid of patches.

In some variants of the model a gradient of numbers was created within the patches. In order to measure this each patch was divided into 4 zones of equal area (each $25m^2$). The zones were all centered on the pitfall trap, the mean step and turn as well as the total number of steps in each zone were recorded.

Results and discussion

In order to compare the results two values were calculated. The first of these was the percentage of the total number of steps (within the trapping area) in each type of patch. This is effectively a measure of density. Second was the percentage of the total number of beetle-metres in each type of patch, a measure of activity. It would also be possible to compare results on the basis of the catch in the pitfalls. However there is a great deal of variation in these results and so the method adopted is preferable, although the results of the section on the relationship between directionality and catch need to be considered. When there was a gradient of activity created within the patch this is taken into account, and only the number of beetle-metres occurring within the central zone of the patch considered.

The results of the various editions of the model are summarised in Table (7.2), each is discussed seperately below.

Table 7.2:

Overall results of the simulation models

			Mean Step	Mean Turn	% Steps	% Bm	% in centre
1	Turn varied, Step constant	1	26	25	50.2	50.2	25
		5	26	110	49.8	49.8	25
2	Turn constant, Step varied	1	48	75	18.8	40.9	24
		5	16	75	81.2	59.1	25
3	Turn varied, Step varied	1	48	25	19.9	42.5	24
		5	16	110	80.1	57.5	26
4	Delay- 5 Step	1	26	25	24.4	19.8	21
	Turn varied, Step constant	5	26	110	75.6	80.2	30
5	Delay- 5 Step	5	48	75	19.3	33.5	21
	Turn constant, Step varied	5	16	75	80.7	66.5	30
6	Delay- 5 Step	1	48	25	8.7	13.1	18
	Turn varied, Step varied	5	16	110	91.3	86.9	33
7	Delay- 2 Step	1	48	25	9.2	17.5	19
	Turn varied, Step varied	5	16	110	90.8	82.5	28
8	Delay- 10 Step	1	48	25	8.1	11.6	17
	Turn varied, Step varied	5	16	110	91.9	88.4	35
9	Search- 20% Prob., 5 Step	1	26	25	36.3	33.0	23
	Turn varied, Step constant	5	26	84	63.7	67.0	26
10	Search- 20% Prob., 5 Step	1	48	75	33.2	45.7	25
	Turn constant, Step varied	5	27	75	67.8	54.3	26
11	Search- 20% Prob., 5 Step	1	48	25	28.3	39.3	23
	Turn varied, Step varied	5	27	84	71.7	60.7	25
12	Search- 40% Prob., 5 Step	1	26	25	30.0	26.0	22
	Turn varied, Step constant	5	26	106	70.0	74.0	26
13	Search- 40% Prob., 5 Step	1	48	75	22.7	39.9	22
	Turn constant, Step varied	5	19	75	77.3	60.1	26
14	Search- 40% Prob., 5 Step	1	48	25	15.2	25.9	21
	Turn varied, Step varied	5	19	106	84.8	74.1	28
15	Search- 5% Prob., 5 Step	1	48	25	43.8	47.5	25
	Turn varied, Step varied	5	41	44	56.2	52.5	25

1)Instant changes in parameter at borders

The first method of attempting to increase the catch in certain
patches was to change the type of movement in each patch. There were
three different possibilities which were considered:

1a) Turn varied, step constant: In this type the step length was kept
the same (mean 25cm) in all patches, but the turn varied so that in
the beetle moved directionally in type 1 patches and with low
directionality in the other. As can be seen in Table (7.2) there is
no difference between the numbers caught in each type of patch,
density and activity being the same in each.

The cause of this is a boundary effect as the beetles attempt to
move from one patch to another. As an individual moves from a
directional to a non-directional patch then there is a high chance of
it moving back across the boundary. Upon entering the patch it turns
through a large angle and returns to the directional patch, and with
high directionality it now heads away from the 'random' patch.
Individuals which succeed in entering deeper into the 'random' patches
stay within these areas for long periods of time. Thus beetles move
rapidly across directional patches, and slowly through random ones,
but because of the high probability of staying in the directional
patches, the total amount of activity is approximately the same in
each.

Suprisingly this mechanism occurs regardless of the sizes of the
different turns. Although the chance of rebounding is lower if the
difference between them is smaller, so would the difference in
effective speed across the patches. The outcome is that density is
always the same if the angle of turn is the only difference between

the patches.

This phenomenon was further investigated by studying the behaviour of beetles at the boundaries. This was done by drawing the tracks of individuals as they crossed the boundaries, the effect was then clear.

1b) Step varied, turn constant: This is the reverse of the above, with a constant turn of 75° in all areas. It is similar to a situation where the beetles maintain the same degree of directionality but are more active in certain patches. Table (7.2) shows that this does produce different densities of beetles in the different areas. However the numbers of beetles caught in the pitfalls are much more similar, because although there are fewer beetles in the long-step patches, these are more active.

1c) Turn and step varied: This is the final type in this group. In patch-type 1 the beetles move directionally and with high speed, whilst in patch-type 5 the opposite occurs. This is closest to the situation which is likely to occur in the field and it has been shown that carabids move more directionally in unsuitable habitats (Baars 1979).

The results from this simple model are, however, very similar to the previous one. Although different densities are created , this effect is cancelled out by the greater distances covered in the low density areas. Although reduced, the boundary effect is still important and the difference in actual catch in the two patches is further reduced by the difference in turn.

In order to further increase the differences between the patches two modifications were made, these eliminated or reduced the boundary effect. In the first, a delay was incorporated so that the parameters of movement did not change instantly upon changing patches, instead the carabid continued walking for a number of steps with the previous dispersal pattern. Thus an individual moving from a directional to a random area would continue walking directionally, after a set number of steps it would switch to more random behaviour. By this time it would be some distance from the border, and hence there was little chance of it moving out again immediately.

The second method adopted was that the beetles moved directionally and with long steps continually, however in some areas (patch-type 5) there was a fixed probability of switching to more random, short step behaviour. The points at which this occurred were not fixed, effectively being scattered at random withn the area, and after a fixed number of steps the beetles would switch back to directional walk.

The first of these models is equivalent to a situation in which beetles do not change their behaviour as soon as they change their their habitat, e.g. moving from an area of luxuriant cabbage to a sparse one a carabid would not commence directional movement until after a few steps. The second resembles more of a restricted search approach. In areas with plenty of cabbage beetles are more likely to find a prey item and hence change their movement patterns.

The results of the delay model will be discussed first. As previously there are three different variations.

Delayed changes in parameter at the borders.

2a) Turn varied, step constant: As can be seen from Table (7.2) the inclusion of the delay has a dramatic effect on the results of the model. Without the boundary effect the slower speed across the patch of the beetles in the patch-type 5 increases the density in these areas. There are three times as many beetles in the random areas, with activity the same.

The delay has another effect, it creates a gradient of beetles across the patches. This is because individuals moving from the random areas continue their high turn rate, producing large numbers of beetles near the edge of the patch. The beetles moving directionally into the random areas penetrate deeper towards the centre, meaning that there are fewer near the edge than in the centre. When this effect is taken into account the difference between the catch in two patches is further accentuated, so 4 times as many are caught in patch-type 5.

2b) Turn constant, step varied: Although this was marginally the most effective variation in the previous model. The delay does little to improve it, as previously the boundary was unimportant. However becuase of the gradient produced there is some improvement in the difference in numbers of beetle caught, with twice as many in patch-type 5.

2c) Turn and step varied: With the boundary effect eliminated the reduction in step length and increase in turn have cumulative effects. Both reduce the effective speed of beetles in the short-step high turn areas and so there is a large difference in density in the two areas. They also both serve to increase the proportion in the central zone of patch-type 5 (and vica versa). Thus, despite the effect of

activity, there is a large difference in the numbers caught in the two zones.

Table (7.2) also shows the effect of changing the length of the delay i.e. the number of steps that the behaviour continues after changing patches. With a very short delay the boundary effect is much reduced, and so the two step delay has a large effect. Increases beyond this do not have a corresponding effect, and very long delays would have the opposite effect. Since within the model a step simulates two minutes activity it is unlikely that any change in behaviour would be delayed beyond a few steps. From a theoretical point of view there is no advantage to be gained from increasing the delay beyond this.

Restricted search model

With this model it was found that high rates of encounter were necessary to create the differences between the two patches. Thus probabilities of 20% and 40% were used, with an effect lasting for 5 steps. The results are shown in Table (7.2), and the three variants discussed below.

3a) Turn varied, step constant: This will produce diffferences between the two patches. As in the previous occasions because the activity is the same in both areas the difference in catch is marked. At the higher probability the difference is increased, though not in proportion.

3b) Turn constant, step varied: Although this produces a larger

difference in numbers between the two areas, th difference in catch is ·
much smaller . This is the result of the higher activity in the low
density areas.

3c) Turn and step varied: Perhaps surprisingly this is nó more
effective than the first variation in producing different catches.
The cause is the same as in the variation above.

Overall it can be seen that it is possible to create differences
in the catch in different areas of traps, using fairly simple
behavioural methods. These reflect the possibilities which exist for
an individual in a patchy field situation. The most effective is the
delay and this is pehaps the simplest on a behavioural level. The
high level of encounter in the restricted search model is not
necessarily unrealistic. Although an animal is unlikely to find prey
items with such regularity, it does resemble the behaviour which
occurs on encounter with a potential food site. Carabids spend much
of their time searching around the base of cabbages, in open areas
they are more likely to move with greater directionality. Within a
brassica field the probability of encountering a cabbage is obviously
high. However at these encounter levels the model becomes similar to
the delay model as the beetles inside the areas with lots of cabbage
move with short step/high turn all the time. Also as the frequencies
increase the boundary effect also becomes more important, reducing the
difference between the patches. This is because with a very high
frequency of encounter the beetle is extremely likely to meet a
cabbage and commence random turn on its first step into the patch.

Having used the model to develop methods of producing variation

in the pitfalls, it is then possible to use these in the full Staddon Heights 1985 program. The aim is to recreate a similar overall daily displacement and also the pattern seen in the recaptures. It is also neccessary to maintain the variation between individual carabids seen at the site; some beetles were caught in the trap grid many weeks after release and others moved to the gutters within a few days. Thus some carabids have a daily displacement many hundreds of times greater than others.

Simulations of Staddon Heights 1984

The previous section suggested a number of points. The first of these is that any simulation model, attempting to reproduce results similar to the field, must include either delay or restricted search type effects. Incorporating the delay effects into the Staddon Heights model is simple, the delay can be the same regardless of the difference between the two adjoining patches. With the alternative model the extremes of movement (patch-types 1 and 5) were kept. In patch-type 5 the encounter rate was high (40%) whilst in the other types of patch this frequency was reduced in steps, so that in patch-type 1 it was only 4%.

These two types of model each have an effect on the dispersal abilities of individuals. The aim is to allow beetles to travel rapidly across patch-type 1 and to create high densities in patch-type 5. A delay has an effect inhibiting rapid movement across some areas, an effect that the restricted search should be less likely to produce.

The models also have to be of the 'turn and step variable' type. It is unrealistic to expect carabids to maintain one or both of these factors constant in different types of habitat. The differences are

also neccessary in order to create the difference in displacement rates between individuals which is apparent in the field.

Before discussing the results of such simulations another model must be described. It was found that using the above effects did not produce entirely satisfactory results and so the model was changed so that it incorporated an orientation mechanism. In this the beetles could choose between patches and if a 'better' patch was close by then they could move towards it. The 'best' patch was patch-type 5 the 'worst' patch-type 1. The distance over which the beetles could sense a patch was variable and the probability of moving towards a patch depended on the difference between the two patches. Thus although there was a high probability of moving into a patch-type 5 if the beetle was in a patch-type 1, the probability of moving into a patch-type 3 from a patch-type 2 was much lower. If the beetles had a choice then they would head towards the better patch. Finally a mechanism was added so that the beetles could ignore the patch value and move away from good patches into bad ones, the probabilty of so doing being variable.

The orientation mechanism had to be used in conjunction with the delay or restricted search model. Otherwise the boundary effects would become an influence. It must be remembered that the addition of this mechanism gives total control over the distribution and movements of the beetles and thus any desired result could be produced by changing the distances over which the beetles react, the probability of them reacting and the probability of them ignoring the patch value.

The results of simulations of Staddon Heights incorporating the above effects are shown in Table (7.3) and Fig. (7.4)

TABLE 7.3:

Results of simulations of Staddon Heights 1985

Delay model;

	No.	Mean m/day	Min. m/day	Max. m/day	Time days	Min. days	Max. days
Uncaught	38	0.96	0.13	2.96			
Pitfalls	49	2.98	0.15	18.03	11.24	1.0	33.0
Gutters	13	4.46	1.39	14.24	14.62	3.0	34.0

Restricted search model

	No.	Mean m/day	Min. m/day	Max. m/day	Time days	Min. days	Max. days
Uncaught	39	1.27	0.12	2.84			
Pitfalls	43	2.37	0.23	11.18	12.98	1.0	35.0
Gutters	18	3.32	1.19	7.86	18.06	6.0	34.0

Orientation model

	No.	Mean m/day	Min. m/day	Max. m/day	Time days	Min. days	Max. days
Uncaught	54	0.98	0.04	2.30			
Pitfalls	36	1.43	0.26	3.61	14.17	2.0	32.0
Gutters	10	1.90	1.26	3.10	25.00	13.0	35.0

Orientation model, with mechanism to ignore orientation

	No.	Mean m/day	Min. m/day	Max. m/day	Time days	Min. days	Max. days
Uncaught	48	1.09	0.06	2.32			
Pitfalls	41	2.29	0.25	15.00	13.44	1.0	35.0
Gutters	11	2.88	1.44	8.06	19.36	5.0	28.0

<u>Figure 7.3</u>:

Distribution of recaptures, model

```
50m   1     0  0  0  1  0
40m   3     1  0  3  1  0
30m   1     0  2  3  0  1
20m   4     2  0  9  4  2
10m   3     0  1  5  2  2
 0m   4     0  0  1  0  0

            1  0  0  1  0
```

This is an example of one of the simulation runs, there was much variation but the same pattern remained throughout.

<u>Table 6.4</u>:

Simulations of Rumleigh 1986, distribution of trapped individuals

Dist from Barrier	% total catch			Catch/trap		
	Bar.	5m	10m	Bar.	5m	10m
Patch 2	86	15	1	2.80	0.68	0.13
Patch 4	71	20	9	2.40	0.91	1.13

Results and discussion

From the figures it can be seen that it is possible to produce a similar pattern in the recaptures to that seen in the field, although there is obviously a great deal of variation between individual runs of the model. The mean daily displacement to those captured in the pitfalls, whilst the displacement to the gutters, although higher than to the pitfalls, is rather low. The model results are most similar to the last release of P. melanarius at Staddon Heights (Table 5.10).

Without much more data it is difficult to distinguish between the various models. However it seems unlikely that models without the orientation mechanism can ever reproduce the field data accurately. This is because there is no method of preventing beeetles moving into certain areas, only of manipulating their behaviour once they are there. In the total field results there was a tenfold difference in catch between traps which were only 20m apart. Allowing the beetles orientation can be used to prevent carabids moving from high density areas into low ones. In the field this could either be a situation where carabids do actively move towards certain areas, or one in which beetles leaving good patches turn back (or both). The simulation effectively covers both these possibilities.

Thus it would appear from these simulations that carabids are likely to posses an ability to orientate towards certain areas. In a cabbage field this is likely to be both individual plants as well as the silhouette formed by a strong growth of plants alongside a sparse patch.

Simulations of Rumleigh, including a barrier

Method

In this model the beetles were prevented from moving beyond the barrier. Inside the plot were 60 pitfall traps, arranged in the same way as at Rumleigh 1985. Behaviour at the barrier was simulated using only simple techniques. At first the beetles simply bounced off the barrier, upon encountering it the next step was in any direction except through the barrier. In order to increase the number of beetles close to the barrier the orientation mechanism was included. This could either function in a strip alongside the barrier, so that in this region carabids tended to move directly towards it, or in a strip some distance from the barrier. In this case beetles close to the barrier could move with the same pattern as those elsewhere in the plot, but those beteen 0.2m and 0.7m from the barrier tended to move towards it. The width of these strips could be varied, as could the probability of remaining within them.

Results and discussion

Briefly the results are shown in Table (7.3). As can be seen it is possible to recreate the distribution seen in the field using the orientation mechanism. However in the real plot behaviour is likely to be more complex, with beetles moving along the barrier itself. It would be possible to include such mechanisms into the model, though it would become quite complex. If carabids were active only in a very small strip alongside the barrier the number caught in pitfalls would be much reduced.

The effects of time and trap spacing

Apart from investigating the processes involved in the field, in creating differences between pitfalls and simulating the mark/recapture data, the model can also be used to explore other factors. Those discussed below are concerned with the estimates of daily dispersal which the mark/recaptue produced and how they relate to the displacement of the population as a whole. The first which was investigated was the effect of time on the mean daily displacement, i.e. how this varied depending on how long the model was run. The second factor was the effect of trap spacing on the mean daily displacement. The information from these results was then used to compare the 'real' daily estimate to that estimated from the recaptures.

Method

A simplified version of the model was used. This consisted of 36 pitfalls (6x6 array) regularly distributed, whose spacing was varied. The spacings used were 5m, 10m and 20m. Beetles were released from the centre of the array and four different dispersal rates were used. These were short step/random turn, short step/directional turn, long step/random turn and long step/directional turn. The method of producing each step was the same as that used previously. Thus each of the four displacement rates were based on the same five sets of limits but the frequency distributions were changed. This allowed a certain amount of individual variation, whilst maintaining the overall effect on displacement rates.

To investigate the influence of time the model was run with the

long step/directional turn and with 10m trap spacing. Beetles were allowed to move for 3, 7, 14, 21 or 35 days.

The effect of trap spacing was tested as follows. For each combination of step length/turn and trap spacing three runs of the model were made. Each consisted of 100 beetles allowed to roam freely, for 3 weeks, there being no limits on the distance moved. There was no patchiness in the model, so the same dispersal rates occurred throughout.

The 'real' displacement rate was calculated in a situation with no traps, fifty individuals were released from a central point and allowed to disperse freely. For each step/turn combination or length of time the model was run three times.

Results and discussion

Effects of time

Table (7.5) summarises the results of the model. As can be seen the real mean daily displacement is very high for the first few days but then drops off rapidly. One cause of this is the effective random turning of the beetles. After the first day mean displacement is high as there is a high probability of moving away from the release point. In the following days the beetles become progressively more spread out (the variance of the displacement increases), and so the mean displacement each day is reduced.

The effects of this on dispersal estimates of the trapped beetles can also be seen in Table (7.5). After three days the estimate derived from the traps is slightly lower than that in the whole population, but after this it is always an overestimate. The cause of

Table 7.4:

Effect of time, 10m spacing

			TRAPPED			UNTRAPPED		
			Mean			Mean		
	Mean	Mean	Daily	Mean	Mean	Daily	Mean	Real
Days	Step	Turn	Disp	Time	Disp	Disp	Disp	Disp
3	45	25	9.90	1.9	17.7	10.07	30.2	10.55
7	45	25	6.86	3.3	17.2	7.00	49.0	6.35
14	45	25	5.75	5.3	19.5	4.68	65.4	4.33
21	45	25	5.26	6.9	18.4	4.18	87.6	3.55
35	45	25	5.22	8.6	19.6	3.35	117.2	2.84

Table 7.5:

Effect of trap spacing, 21 days

			TRAPPED			UNTRAPPED		
			Mean			Mean		
	Mean	Mean	Daily	Mean	Mean	Daily	Mean	Real
Days	Step	Turn	Disp	Time	Disp	Disp	Disp	Disp
5m	24	25	2.42	6.4	8.9	1.97	41.3	1.80
10m	24	25	2.90	8.3	17.5	1.82	38.1	1.80
20m	24	25	3.52	8.9	20.2	1.84	38.7	1.80
5m	24	95	1.60	7.4	8.4	0.97	20.4	0.83
10m	24	95	1.39	10.6	11.5	0.88	18.5	0.83
20m	24	95	1.49	12.4	15.6	0.85	17.8	0.83
5m	45	25	5.75	3.6	9.5	4.34	91.1	3.55
10m	45	25	5.26	6.9	18.4	4.18	87.6	3.55
20m	45	25	5.23	10.9	36.1	3.76	78.9	3.55
5m	45	95	3.37	3.8	8.7	1.76	36.8	1.53
10m	45	95	2.80	8.3	16.5	1.69	35.4	1.53
20m	45	95	2.40	11.5	24.2	1.48	31.1	1.53

the initial overestimate is that the beetles are intercepted before they reach their mean displacement for the time period. This effect would be much more marked after one day, but could be reduced if it the time to capture was averaged (i.e. half a day) (Hawkes 1972). The subsequent overestimates are due to two interacting factors. The first of these is that beetles remaining close to the release point (or returning to it) are not sampled by the traps, and these individuals have a very low mean displacement rate. Secondly there is an effect of trapping out individuals which would have remained close to the release point so that these cannot provide a low displacement rate at the end of the model run. This effect is underlined by the mean displacement of the untrapped individuals at the end of the model run (Table 7.5), in all cases after three days this is higher than the real estimate.

Effects of trap spacing

Table (7.6) shows the means of the separate runs, and it is clear that there can be quite large differences between the results of the different trap spacings, despite the fact that identical dispersal rates occurred in each. It should be remembered that some of the estimates are based on very few individuals (particularly the 20m spacing with short/random moving beetles). A number of interacting factors are involved in producing these results, those already outlined above.

The first relates to the probability of being trapped close to the release point. With the 5m spacing there is a relatively high chance of being trapped soon after release, at 20m this chance is much lower. As the individuals are trapped after only a short time their

mean daily displacement is high. This effect can be best seen in the long step dispersal where the 5m spacing produces a considerably larger estimate (Table 7.6).

A conflicting factor is produced by the variation within the dispersal rates of individuals produced by the model. Under all four rates daily displacement can vary widely. This effect can be best seen in the short step dispersal. Those individuals which are captured in the 20m and 10m traps form the extreme of the population, those moving with the greatest daily displacement. Thus there is a very biased sample in these traps, whilst the 5m traps sample the population as a whole. This factor will also have the reverse result; the 5m traps may tend sample a biased proportion, the most rapidly moving individuals having left the grid.

Table (7.6) also shows the effect of the different trap spacings on the estimated and real daily displacements. As can be seen, without exception the estimates from the recaptures are over-estimates of the real value.

The causes of this are related to the factors in the previous section, although the mechanisms are different.

At high trap densities (i.e. 5m) a large proportion of the released population is trapped out, the chances of an individual remaining within the trap grid for the whole period are low. A beetle captured soon after release is likely to have a high daily displacement because of the effect of time. Also those individuals which remain untrapped for a long period have a very low daily displacement, this has a large effect on the results of the population as a whole. The effect can be seen by comparing the displacement of the individuals which were not caught with the actual value. In most cases it is higher, more so with the 5m grid, thus many of those

within the area of the grid were removed. The result is to increase the difference between the estimate from the trapped beetles and the actual displacement.

With the 20m spacing the estimate may be too high for another reason. As discussed previously this is because the pitfalls sample a biased proportion of the beetles. Although the beetles which remain close to the release point are not trapped out, they are missed because they can never be sampled!.

There is no simple resolution to these consequences of trapping in order to estimate a daily displacement. A trapping grid could be produced with irregular trap spacing, and possibly with traps which were placed close to the release point some time after the release occurred. This might allow more accurate estimates to be produced. However in the field, using a regular grid, a much lower proportion of the population will be caught in the traps and so the effect of trapping out will be lower. The model shows that a larger distance between traps produces a more accurate estimate of dispersal. Against this, however, there is the problem of recapturing a large enough sample for an accurate estimate.

Overall the model proved a useful tool in exploring some of the factors involved in the field results. However there are a number of problems remaining, though none of these affect the general conclusions.

The first of these is that the models always produce too many recaptures, compared to the field data. There could be a number of reasons for this. Obviously the probability of recapture may be too high, though Luff (1975) suggests that for glass pitfalls the

efficiency is higher than that used in the model (see Section 4.7).
Alternatively the activity may be too high. In the model the beetles
move in straight lines for each two minute period and effectively
cover a 1cm wide area. In the field individuals do not move in
straight lines and 1cm is probably an underestimate of their effective
width. The effect of this should be to increase the catch in the
field relative to the model. Without a great deal of further work
tracking beetles at night, with shorter periods between points, it is
not possible to offer a firm resolution as to the differences between
the model and the field. However it seems that the parameters of
movement used in the model are at least rough approximations of those
in real life, as the daily displacements are similar. Thus it would
appear that the traps are less efficient than might appear. A
further, and possibly very important, factor is that there was no
mortality in the model, whilst in the field this was likely to be
high, at least at certain times.

8.1 General discussion

Evans (1983) describes some of the complex cues some carabids may use to identify appropriate habitats. The work shows that hygrophilous species are attracted by volatile metabolites of certain algae, which are associated with their habitates. Evans (1983) differentiates between directional stimuli (odours, light etc.) which enable carabids to locate their habitats, and non-directional stimuli (humidity, heat, light intensity), which produce kinetic responses to maintain body temperature and other such factors. Carabids within a brassica field respond to a similar set of factors.

The first sections of the results showed that many species are associated with one particular part of the field, and that there was also patchiness within the crop itself. Thus the carabids are likely to be able to identify differences within the habitat. Whether this is a response to micro-habitat, prey distribution or some complex environmental cue is unknown. Kooijman and Hengeveld (1979) attempted to describe the distribution of certain carabids in grassland in a model, using a non-linear relationship between environmental variable and numbers. The results were not entirely satisfactory, but led to the suggestion that the distribution of carabids was related to the water content in the soil. Patchy distribution of carabids has also been produced by creating artificial patches of prey (Bryan & Wratten 1984).

The simulation model has demonstrated what kinds of changes in movement patterns would be needed in order to produce the differences in pitfall catches which were seen in the field. The underlying mechanism behind these changes is probably that described by Grum (1971, 1975), who first showed that there is an increase in mobility

involved in the probability of a carabid encountering a trap. The highest catch in any grid of pitfalls is in the area where the combination of density and activity produces the highest amount of total distance covered on the ground (allowing for the effect of turn). The model was adapted so that the highest catch was in the areas with the highest density beetles, but this may not be the case in the field. Although unlikely it is possible that there are areas where there are very high densities of very inactive beetles and it is not possible for pitfalls to locate these. Greenslade (1964a) suggested that catch will be reduced in areas of high plant density (i.e. weedy or in grass), though this will only be the case if the total distance covered by each indivdual is reduced. In such areas it is possible that there is more prey available, reducing activity, or that turn rate is higher. Further, many of the carabids might climb amongst the plants, above the soil surface. Clearing an area of ground around each trap (Greenslade 1964a) prevents beetles climbing above the traps and reduces any possible effect of speed of movement of carabids as they encounter the traps.

The model also suggests that traps with a small surface relative to perimeter are advantageous, as the catch is related to the perimeter but a small surface reduces the effects due to different turn rates. However non-circular traps are influenced by any tendency for carabids to move in particular directions, and glass is the most effective material for traps (Luff 1975), and so circular, glass pitfalls remain the most effective.

Another point is that the increases in certain pitfalls in the model is not due to any tendency for the beetles to move in a particular direction, this being random. Thus in the field higher recaptures in certain areas should not necessarily be intepreted as

non-random directions of dispersal (or lack of) (Greenslade 1964b, Ernsting 1978)

In terms of the difference in recaptures of P. melanarius and H. rufipes this is most likely to be due to the difference in total ground covered found during the individual tracking (Section 6). The difference in overall directionality also reduces the relative catch of H.rufipes, and at Rumleigh the behaviour at the barrier would be a large influence on the results. The work further empthasizes the dangers in using pitfalls to compare species (Greenslade 1964a). However the traps would be much more effective if data on mean activity and turn (e.g. by tracking) could be obtained.

Janzen & Metz (1979) produce a mathematical model of pitfall trapping and suggest that both density and activity can be estimated from the results, though not with any accuracy. If either density or activity (including turn) is known then it should be possible to estimate the other parameter using models, such as that produced in this study.

Taylor (1986) defines dispersal as movement occurring in response to other individuals and is an "active centrifugal movement, reducing local density". He states that the estimates of displacement made by releasing marked individuals from a central release point (such as Dobzhansky & Wright 1943) are measuring dispersal in this sense. However it is legimate to question whether the movement of individuals, following such a release, is in fact a response to the presence other individuals. If this were the case then density-dependant effects of release would be expected, with rate of dispersal being related to the numbers released. However, in cabbage root flies at least, this is not the case (Hawkes pers. com.)

As far as this study is concerned it might be considered that the

movement patterns were primarily the product of foraging, together with other factors such as reproductive behaviour and 'escape' responses from unsuitable patches. Although the model makes no assumptions about the underlying causes of movement, the majority of individuals were moving so as to increase the density in certain areas. The tracking of individuals at night suggested that there are no immediate effects of contact with other carabids, but it seems likely that factors such as hunger are a much more important influence on carabid activity.

Whether the displacement rates produced were the product of 'dispersal' or of foraging behaviour is basically an etymological argument. However it is an underlying assumption of the model that there are no 'dispersive' individuals. Much of the work on dispersal has been in relation to population ecology (Hassell 1980, Horn 1983) and the importance of dispersers in maintaining overall population stability.

In this respect the ecology of flightless species of carabid, such as P. melanarius should be considered. As polyphagous predators, common in a wide variety of agricultural and other habitats, populations are likely to be relatively continuous over wide areas. Adults have the ability to cover relatively long distances by walking and this is likely to be sufficient to repopulate any localised areas which became depopulated. Thus the advantages of dispersal in species which occupy unstable or very patchy habitats (Southwood 1962) are not present in carabids like P. melanarius.

The foraging pattern is likely to be associated with the distribution of prey items. Under all circumstances this is likely to be patchy (on many different levels). The simulation model suggested that the reason for the different catches of P. melanarius and

H. rufipes is related to their movement patterns. Although there is no data on the distribution of prey it seems reasonable to suggest that the movement pattern of P. melanarius could be related to the unpredictable distribution of patches which are not likely to be renewed. These could range from clumps of eggs to lepidopteran larvae. Particularly at Rumleigh however H. rufipes was found feeding on seeds which had fallen to the ground and these patches are likely to be renewed regularly. Under these circumstances a more restricted search pattern is appropriate.

The boundary effect produced by changing turn size in different patches of the model is interesting in a wider sense. It suggests that simple behavioural mechanisms such as turning will not serve to keep individuals in certain areas. Thus mechanisms such as klinokineses may be more complicated than first appears.

Apart from the problem of defining disersal there is also a problem in quantifying it. The main method, other than simply dividing distance covered by time as has been done in previous sections, is to fit some density-distance relationship to the data. There are a number of equations (Taylor 1978) which describe the data with varying degrees of success. A value for displacement per day can then be produced by integration (Hawkes 1972, Robinson & Luff 1979). Although this would be possible for the data produced in this study it has not been done as there are relatively few recaptures at each site. However Hawkes (pers. com.) has shown, using simulation models, that this method produces an overestimate of the actual mean displacement, as does the simple method.

Beyond this the mean displacement each day depends on the time scale chosen, although this is less important if long time periods are used. The mean displacement each day, which is just a few metres for

carabids, does not reflect the very long distances which some
individuals will cover.

Because of these problems the simulation model approach is
probably the most useful. Ideally individual simulation models could
be created to mirror each situation being investigated. However,
practically simulation models using a random diffusion type process
will produce results which are very close to the field situation
(Kareiva 1982, 1983). This is not because the animal moves at random
(purely random movement is likely to be extremely rare) but the
overall effect over long time periods is to produce a process which
can be described in this way.

Acknowledgements

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Appendix 1

Statisical analysis

In Section 4.5 (pg. 120) the data from the pitfall captures was analysed using Analysis of Variance. As the data was not normally distributed a transformation was necessary, the one used was derived from Taylor's Power Law (Southwood 1978).

In order to do this the data was first summed over each week for each trap. To provide a mean and variance all the traps in each grid were summed. The transformation used was direct from the Power Law, rather than using an approximation (such as square root). After the transformation the relationship between the mean and variance was checked, as these should be independent. However in almost all the cases there was still a significant relationship. This could have been cancelled by further pooling of data. However, as interactions between time and space were the main rationale behind the analysis, this would have rendered the exercise pointless.

Thus the analysis must be viewed in the knowledge that the data was not normal, though the test is a robust one.

The analysis itself was carried out using the GENSTAT anova routine.

Appendix 2

Recaptures of marked beetles

Individually marked Nebria brevicollis, Battisborough Cross 1983

Rel.	Date	Rec.	Date
FH	24/5	FH	15/5
FH	27/5	FP	7/11
FH	3/5	CE	17/9
C0	24/5	CE	28/9
C10	19/5	FH	25/5
C10	19/5	CG	30/9
C10	24/5	FH	1/6
C10	24/5	CE	3/10
C10	3/6	CH	21/9
C10	8/6	CE	30/9
C20	27/5	CE	3/10
C20	3/6	C20	13/6
C20	3/6	FP	23/9
C20	24/5	C20	25/5
C50	3/6	CH	15/6
C50	10/6	FP	26/9

In the following pages the recapture data for Rumleigh 1985 is
presented in full for the three species P. melanarius, P. cupreus
and H. rufipes. The data includes the time to recapture, the total
displacement and the mean displacement each day (Distance/time).
In P.cupreus there was high mortality of the first releases in the
traps, and so some of the numbers were used a second time.

Pterostichus melanarius

No	Rel	Date	Rec	Date	Days	Disp	m/day
4	MID	5/6	K3	12/7	36.5	22.5	0.62
6	MID	12/6	J1	26/6	13.5	20.2	1.50
6	J1	26/6	C1	28/6	1.5	35.0	23.33
6	C1	28/6	C2	1/7	2.0	5.0	2.50
7	MID	12/6	A1	28/6	15.5	29.3	1.89
7	A1	28/6	C4	29/7	30.0	18.0	0.60
8	MID	12/6	H1	19/6	6.5	12.5	1.92
9	MID	12/6	B4	1/7	18.0	23.0	1.28
11	MID	21/6	A1	24/6	2.0	29.3	14.65
11	A1	24/6	E1	3/7	8.5	20.0	2.35
12	MID	21/6	H4	19/7	27.5	9.0	0.33
13	MID	21/6	I2	24/7	32.5	13.5	0.42
15	MID	21/6	G1	28/6	6.5	10.3	1.58
16	MID	21/6	E5	5/7	13.5	12.5	0.93
17	MID	21/6	G4	1/7	9.0	5.6	0.62
17	G4	1/7	L5	5/7	3.5	25.5	7.29
18	MID	21/6	K5	28/6	6.5	24.6	3.78
19	MID	21/6	K1	26/6	4.5	24.6	5.47
19	K1	26/6	B5	1/7	4.0	49.2	12.30
24	MID	21/6	G2	1/7	9.0	5.6	0.62
26	MID	21/6	L5	17/7	26.5	29.3	1.15
27	MID	21/6	L4	3/7	11.5	28.0	2.43
27	L4	3/7	K3	19/7	15.5	7.1	0.46
27	K3	19/7	L2	29/7	9.5	7.1	0.75
28	MID	21/6	C5	3/7	11.5	20.2	1.76
29	MID	21/6	G3	28/6	6.5	2.5	0.38
29	G3	28/6	D4	3/7	4.5	15.8	3.51
30	MID	21/6	B4	22/7	30.0	23.0	0.77
32	MID	21/6	C3	5/7	13.5	27.5	0.74
33	MID	21/6	C3	5/7	13.5	17.5	1.30
36	MID	24/6	C1	26/6	1.5	20.2	13.47
36	C1	26/6	A1	28/6	1.5	10.0	6.67
37	MID	24/6	H3	26/6	1.5	7.5	5.00
40	MID	24/6	E1	1/7	6.0	12.5	2.08
40	E1	1/7	F1	3/7	1.5	5.0	3.33
41	MID	24/6	L1	3/7	8.5	29.3	3.45
44	MID	24/6	A3	8/7	13.0	27.5	2.12
45	MID	24/6	A4	5/7	10.5	28.0	2.67
46	MID	24/6	I1	26/6	1.5	16.0	10.67
46	I1	26/6	F1	1/7	4.0	15.0	3.75
46	F1	1/7	F1	3/7	1.5	0.0	0.00
48	MID	24/6	G3	26/6	1.5	2.5	1.67
49	MID	24/6	D2	7/8	43.5	13.5	0.31
52	MID	24/6	L3	2/8	38.5	27.5	0.71
55	MID	24/6	L3	28/6	3.5	27.5	7.86
55	L3	28/6	L2	5/7	6.5	5.0	0.77

Pterostichus melanarius

No	Rel	Date	Rec	Date	Days	Disp	m/day
55	L2	5/7	L2	8/7	2.0	0.0	0.00
56	MID	24/6	K5	21/8	57.5	24.6	0.43
58	MID	24/6	J1	28/6	3.5	20.2	5.77
58	J1	28/6	L3	1/7	2.0	14.1	7.07
59	MID	24/6	L1	8/7	13.0	29.3	2.25
60	MID	24/6	G3	26/7	1.5	2.5	1.67
63	MID	24/6	L3	5/7	10.5	27.5	2.62
64	MID	24/6	D3	26/7	31.5	12.5	0.40
64	D3	26/7	C5	12/8	46.0	11.2	0.24
64	C5	12/8	H4	14/8	1.5	25.5	17.00
65	MID	24/6	G3	26/6	1.5	2.5	1.67
65	G3	26/6	F5	3/7	6.5	11.2	1.72
66	MID	24/6	L1	5/8	10.5	29.3	2.79
69	MID	24/6	C2	31/7	36.5	18.2	0.50
76	MID	24/6	G5	19/7	24.5	10.3	0.42
77	MID	24/6	E2	28/6	3.5	9.0	2.57
77	E2	28/6	D1	3/7	4.5	7.1	1.57
78	MID	24/6	E5	28/6	3.5	12.5	3.57
78	E5	28/6	F5	3/7	4.5	5.0	1.11
78	F5	3/7	F5	5/7	1.5	0.0	0.00
82	MID	24/6	G5	1/7	6.0	10.3	1.72
83	E2	28/6	D1	3/7	4.5	7.1	1.57
84	MID	10/7	K3	22/7	11.0	22.5	2.05
86	MID	10/7	K3	26/7	15.5	22.5	1.45
88	MID	10/7	A2	17/7	6.5	28.0	4.31
88	A2	17/7	I1	2/8	15.5	40.3	2.60
88	I1	2/8	E5	12/8	9.0	28.3	3.14
88	E5	12/8	E3	4/9	6.5	10.0	1.54
88	E3	4/9	D5	9/9	4.5	11.2	2.48
90	MID	10/7	K5	2/8	22.5	24.6	1.09
90	K5	2/8	K5	12/8	9.0	0.0	0.00
91	MID	10/7	C5	22/7	11.0	20.2	1.84
92	MID	10/7	B3	12/8	32.0	22.5	0.70
96	MID	10/7	H2	24/7	13.5	9.0	0.67
96	H2	24/7	K3	29/7	4.0	15.8	3.95
96	K3	29/7	F2	5/8	6.0	25.5	4.25
96	F2	5/8	C4	12/8	6.0	18.0	3.01
99	MID	10/7	G5	5/8	25.0	10.3	0.41
99	G5	5/8	I2	16/8	10.5	18.0	1.72
101	MID	10/7	I2	21/8	41.5	13.5	0.33
103	MID	10/7	I2	9/8	29.5	13.5	0.46
103	I2	9/8	K5	14/8	4.5	18.0	4.00
104	MID	10/7	L2	31/7	20.5	28.0	1.37
104	L2	31/7	L5	9/8	8.5	15.0	1.76
108	MID	10/7	I5	19/7	8.5	16.0	1.88
113	MID	10/7	L4	29/7	18.0	28.0	1.56
113	L4	29/7	K5	12/8	13.0	7.1	0.54
113	K5	12/8	L4	14/8	1.5	7.1	4.71
115	MID	10/7	L3	31/7	20.5	27.5	1.34
116	MID	10/7	F2	31/7	20.5	5.6	0.27

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No	Rel	Date	Rec	Date	Days	Disp	m/day
116	F2	31/7	E1	5/8	4.0	7.1	1.77
118	MID	10/7	K2	26/7	15.5	23.0	1.48
119	MID	10/7	H4	29/7	18.0	9.0	0.50
120	MID	10/7	H2	24/7	13.5	9.0	0.67
120	H2	24/7	D2	9/8	15.5	20.0	1.29
120	D2	9/8	J3	14/8	4.5	30.4	6.76
124	MID	10/7	I4	24/7	13.5	13.4	0.99
124	I4	24/7	I4	31/7	6.5	0.0	0.00
127	MID	10/7	E2	31/7	20.5	9.0	0.44
133	MID	10/7	A4	17/7	6.5	28.0	4.31
134	MID	10/7	D4	9/8	29.5	13.5	0.46
134	D4	9/8	C4	12/8	2.0	5.0	2.50
134	C4	12/8	A3	19/8	6.0	11.2	1.86
134	A3	19/8	B4	21/8	1.5	7.1	4.71
134	B4	19/8	B5	23/8	3.5	5.0	1.43
135	MID	10/7	L2	29/7	18.0	28.0	1.56
135	L2	29/7	H4	5/8	6.0	22.4	3.73
136	MID	10/7	K1	31/7	20.5	24.6	1.20
136	K1	31/7	J1	2/8	1.5	5.0	3.33
136	J1	2/8	L3	14/8	11.5	14.1	1.23
138	MID	10/7	J2	2/8	22.5	18.2	0.81
142	MID	10/7	L2	29/7	18.0	28.0	1.56
142	L2	29/7	K2	31/7	1.5	5.0	3.33
143	MID	10/7	E5	29/7	18.0	12.5	0.69
145	MID	10/7	I2	2/8	22.5	13.5	0.60
146	MID	10/7	D2	5/8	25.0	13.5	0.54
149	MID	10/7	D5	29/7	18.0	16.0	0.89
149	D5	29/7	C4	5/8	6.0	7.1	1.18
151	MID	10/7	E3	24/7	13.5	7.5	0.56
151	E3	24/7	B3	31/7	6.5	15.0	2.31
151	B3	31/7	D1	2/8	1.5	14.1	9.43
151	D1	2/8	E3	12/8	9.0	11.2	1.24
151	E3	12/8	C4	16/8	3.5	7.1	2.02
151	C4	16/8	F3	23/8	6.5	15.8	2.43
154	MID	10/7	J4	29/7	18.0	18.2	1.01
155	MID	10/7	I3	14/8	34.5	12.5	0.36
155	I3	14/8	D4	28/8	13.5	25.5	1.89
157	MID	10/7	B2	31/7	20.5	23.0	1.12
157	B2	31/7	B1	12/8	11.0	5.0	0.45
158	MID	10/7	H2	29/7	18.0	9.0	0.50
158	H2	29/7	L5	5/8	6.0	25.0	4.17
162	MID	10/7	H3	19/7	8.5	7.5	0.88
162	H3	19/7	K3	24/7	4.5	15.0	3.33
162	K2	24/7	I4	29/7	4.0	14.1	3.54
164	MID	10/7	L5	5/8	25.0	29.3	1.17
165	MID	10/7	E3	24/7	13.5	7.5	0.56
165	E3	24/7	F2	26/7	1.5	7.1	4.70
165	F2	26/7	H2	31/7	4.5	10.0	2.22
165	H2	31/7	H3	5/8	4.0	5.0	1.25
165	H3	5/8	A4	14/8	8.5	35.4	4.16

Pterostichus melanarius

No	Rel	Date	Rec	Date	Days	Disp	m/day
166	MID	10/7	E4	24/7	13.5	12.5	0.93
166	E4	24/7	C2	31/7	6.5	14.1	2.17
166	C2	31/7	C2	2/8	1.5	0.0	0.00
166	C2	2/8	C2	5/8	2.0	0.0	0.00
168	MID	10/7	J3	19/7	8.5	17.5	2.06
168	J3	19/7	L2	2/8	13.5	7.1	0.52
172	MID	10/7	C3	31/7	20.5	17.5	0.85
173	MID	10/7	I4	24/7	13.5	13.5	1.00
174	MID	10/7	F3	9/8	29.5	2.5	0.08
182	MID	10/7	G3	17/7	6.5	2.5	0.38
182	G3	17/7	L2	29/7	11.0	25.5	2.32
183	MID	10/7	G5	24/7	13.5	10.3	0.76
183	G5	24/7	F2	2/8	8.5	15.8	1.86
184	MID	5/8	C2	16/8	10.5	18.2	1.73
185	MID	5/8	E4	21/8	15.5	9.0	0.58
185	E4	21/8	D4	28/8	6.5	5.0	0.77
186	MID	5/8	E3	19/8	13.0	9.0	0.69
189	MID	5/8	I2	14/8	8.5	13.5	1.59
189	I2	14/8	E4	21/8	6.5	22.4	3.44
190	MID	5/8	C2	28/8	22.5	18.2	0.81
192	MID	5/8	J3	14/8	8.5	17.5	2.06
193	MID	5/8	L3	16/8	10.5	27.5	2.62
196	MID	5/8	A5	7/8	1.5	29.3	19.53
196	A5	7/8	F5	21/8	13.5	25.0	1.85
197	MID	5/8	J4	14/8	8.5	18.2	2.14
197	J4	14/8	I4	16/8	1.5	5.0	3.33
197	I4	16/8	K5	19/8	2.0	11.2	5.59
198	MID	5/8	L3	12/8	6.0	27.5	4.58
199	MID	5/8	G2	12/8	6.0	5.6	0.93
206	MID	5/8	D5	23/8	17.5	16.0	0.91
207	MID	5/8	D2	14/8	2.5	13.5	1.50
207	D2	14/8	A5	19/8	4.0	21.2	5.30
208	MID	5/8	J2	21/8	15.5	18.2	1.17
208	J2	21/8	G3	23/8	1.5	15.8	10.51
209	MID	5/8	E4	12/8	6.0	9.0	1.50
209	E4	12/8	L2	28/8	15.5	36.4	2.35
210	MID	5/8	J3	9/8	3.5	17.5	5.00
210	J3	9/8	E4	12/8	2.0	25.5	12.75
212	MID	5/8	B3	14/8	8.5	22.5	2.65
212	B3	14/8	B3	21/8	6.5	0.0	0.00
214	MID	5/8	L4	7/8	1.5	28.0	18.67
214	L4	7/8	K4	12/8	4.0	5.0	1.25
214	K4	12/8	H5	19/8	6.0	15.8	2.64
220	MID	5/8	L3	12/8	6.0	27.5	4.58
220	L3	12/8	E4	14/8	1.5	35.3	23.56
221	MID	5/8	L3	14/8	8.5	27.5	3.24
221	L3	14/8	K3	16/8	1.5	5.0	3.33
225	MID	5/8	A5	7/8	1.5	29.3	19.5
226	MID	5/8	B5	12/8	6.0	24.6	4.10
227	MID	5/8	H1	7/8	1.5	12.5	8.33

Pterostichus melanarius

No	Rel	Date	Rec	Date	Days	Disp	m/day
227	L1	9/8	G2	12/8	2.0	25.5	12.75
227	G2	12/8	L2	19/8	6.0	25.0	4.17
229	MID	5/8	D2	23/8	17.5	13.5	0.77
230	MID	5/8	H2	7/8	1.5	9.0	6.00
230	H2	7/8	J1	9/8	1.5	11.2	7.45
230	J1	9/8	H5	19/8	9.0	22.4	2.48
231	MID	5/8	E5	7/8	1.5	12.5	8.33
231	E5	7/8	A1	12/8	4.0	28.3	7.07
232	MID	5/8	L2	7/8	1.5	28.0	18.67
232	L2	7/8	K2	14/8	6.5	5.0	0.77
233	MID	5/8	H3	7/8	1.5	7.5	5.00
233	H3	7/8	G2	12/8	4.0	7.1	1.77
233	G2	12/8	E2	14/8	1.5	10.0	6.67
233	E2	14/8	B2	19/8	4.0	15.0	3.75

Pterostichus cupreus

No	Rel	Date	Rec	Date	Days	Disp	m/day
1	MID	28/5	J2	29/5	1.0	18.2	18.20
1	J2	29/5	J2	12/6	13.5	18.0	1.34
1	A1	24/6	A1	26/6	1.5	0.0	0.00
2	MID	28/5	A1	31/5	2.5	29.3	11.72
3	MID	28/5	L2	17/6	19.0	28.0	1.47
4	MID	28/5	B5	29/5	1.0	24.6	24.60
5	MID	28/5	L1	3/6	5.0	29.3	5.86
6	MID	28/5	K5	31/5	2.5	24.6	9.84
6	K5	31/5	J3	26/6	25.5	11.2	0.44
6	J3	26/6	L5	3/7	6.5	14.1	2.18
7	MID	28/5	F4	29/5	1.0	5.6	5.60
8	MID	28/5	G3	31/5	2.5	2.5	1.00
9	MID	28/5	B2	3/6	6.0	23.0	4.60
10	MID	28/5	B2	29/5	1.0	23.0	23.00
10	B2	29/5	F3	3/6	4.0	20.6	5.16
11	MID	28/5	K1	3/6	5.0	24.6	4.92
12	MID	28/5	B2	3/6	5.0	23.0	4.60
14	MID	28/5	G4	10/7	11.0	5.6	0.51
16	MID	28/5	H1	3/6	5.0	12.5	2.50
17	MID	28/5	L5	3/6	5.0	29.3	5.86
17	L5	3/6	L2	5/7	31.5	15.0	0.48
18	MID	28/5	F1	12/6	14.5	10.3	0.71
18	F1	12/6	L2	21/6	8.5	30.4	3.58
18	L2	21/6	L3	26/6	4.5	5.0	1.11
20	MID	28/5	J1	31/5	2.5	20.2	8.08
21	MID	28/5	G2	31/5	2.5	5.6	2.24
22	MID	28/5	A2	3/6	5.0	28.0	5.60
25	MID	28/5	H1	3/6	5.0	12.5	2.50
26	MID	28/5	K3	17/7	49.5	22.5	0.45
27	MID	28/5	A5	5/6	7.5	29.3	3.91
27	A5	5/6	A5	10/6	4.0	0.0	0.00
29	MID	28/5	G3	3/6	5.0	2.5	0.50
30	MID	28/5	F5	31/5	2.5	10.3	4.12
32	MID	28/5	I3	3/6	5.0	12.5	2.50
33	MID	28/5	J3	10/6	12.0	17.5	1.46

Pterostichus cupreus

No	Rel	Date	Rec	Date	Days	Disp	m/day
33	J3	10/6	F5	26/6	15.5	22.4	1.44
34	MID	28/5	J2	3/6	5.0	18.2	3.64
35	MID	28/5	H2	5/6	7.5	9.0	1.20
36	MID	28/5	A5	5/6	7.5	29.3	3.91
36	A5	5/6	A5	26/6	20.5	0.0	0.00
36	A5	26/6	A5	28/6	1.5	0.0	0.00
37	MID	28/5	F3	26/6	28.5	2.5	0.09
39	MID	28/5	H5	29/5	1.0	12.5	12.50
40	MID	28/5	F3	3/6	5.0	2.5	0.50
42	MID	28/5	G5	31/5	2.5	10.3	4.12
43	MID	28/5	A3	31/5	2.5	27.5	11.00
45	MID	28/5	A1	3/6	5.0	29.3	5.86
46	MID	28/5	G2	29/5	1.0	5.6	5.60
46	G2	29/5	E2	3/6	4.0	10.0	2.50
51	MID	29/5	A3	21/6	22.5	27.5	1.22
51	A3	21/6	A1	26/6	4.5	10.0	2.22
51	A1	26/6	C3	5/7	8.5	14.1	1.66
53	MID	29/5	G5	31/5	1.5	10.3	6.87
54	MID	29/5	A5	31/5	1.5	29.3	19.53
55	MID	29/5	A3	5/6	6.5	27.5	4.23
55	A3	5/6	A3	7/6	1.5	0.0	0.00
55	A3	7/6	A5	17/6	9.0	10.0	1.11
56	MID	29/5	F4	7/6	8.5	5.6	0.66
56	F4	7/6	D1	26/6	18.5	18.0	0.97
56	D1	26/6	H4	1/7	4.0	25.0	6.25
56	H4	1/7	G5	3/7	1.5	7.1	4.71
57	MID	29/5	I1	31/5	1.5	16.0	10.67
59	MID	29/5	G3	31/5	1.5	2.5	1.67
60	MID	29/5	K2	31/5	1.5	23.0	15.33
61	MID	29/5	E3	3/6	4.0	7.5	1.88
62	MID	29/5	K1	3/6	4.0	24.6	6.15
63	MID	29/5	F3	3/6	4.0	2.5	0.63
64	MID	29/5	E1	1/7	32.0	12.5	0.39
64	E1	1/7	E2	15/7	13.0	5.0	0.38
65	MID	29/5	E1	12/6	13.5	12.5	0.93
65	E1	12/6	E1	17/6	4.0	0.0	0.00
66	MID	29/5	E4	12/6	13.5	9.0	0.67
66	E4	12/6	A5	19/6	6.5	20.6	3.17
66	A5	19/6	A4	21/6	1.5	5.0	3.33
68	MID	29/5	K4	3/6	4.0	23.0	5.75
70	MID	29/5	K3	19/6	20.5	22.5	1.10
70	K3	19/6	I3	12/8	53.0	10.0	0.19
72	MID	29/5	I3	31/5	1.5	12.5	8.33
74	MID	29/5	A3	31/5	1.5	27.5	18.33
75	MID	29/5	F5	26/6	27.5	10.3	0.37
76	MID	29/5	B1	31/5	1.5	24.6	16.40
78	MID	29/5	L5	10/6	11.0	29.3	2.66
79	MID	29/5	L3	5/6	6.5	27.5	4.23
82	MID	29/5	J1	3/6	4.0	20.2	5.05
84	MID	29/5	L5	3/6	4.0	29.3	7.33

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No	Rel	Date	Rec	Date	Days	Disp	m/day
84	L5	3/6	L2	17/6	13.0	15.0	1.15
84	L2	17/6	H3	3/7	15.5	20.6	1.33
84	H3	3/7	E3	12/7	8.5	15.0	1.76
85	MID	29/5	E4	31/5	1.5	9.0	6.00
86	MID	29/5	L3	10/6	11.0	27.5	2.50
87	MID	29/5	G2	31/5	1.5	5.6	3.73
88	MID	29/5	A4	21/6	22.3	28.0	1.24
89	MID	29/5	D3	31/5	1.5	12.5	8.33
89	D3	31/5	I3	1/7	30.0	25.0	0.83
90	MID	29/5	K4	3/6	4.0	23.0	5.75
92	MID	29/5	I5	5/6	6.5	16.0	4.00
93	MID	29/5	L2	17/6	18.0	28.0	1.56
94	MID	29/5	J4	31/5	1.5	18.2	12.13
95	MID	29/5	D2	14/6	15.5	13.5	0.87
95	D2	14/6	I5	1/7	16.0	29.2	1.82
96	MID	29/5	B3	7/6	8.5	22.5	2.65
98	MID	29/5	L2	5/7	36.5	28.0	0.77
101	MID	29/5	A3	5/6	6.5	27.5	4.23
102	MID	29/5	L2	3/6	4.0	28.0	7.00
102	L2	3/6	A3	28/6	24.5	55.2	2.25
102	A3	28/6	A5	22/7	23.0	10.0	0.43
102	A5	22/7	A5	24/7	1.5	0.0	0.00
102	A5	24/7	A5	2/8	8.5	0.0	0.00
103	MID	29/5	A5	31/5	1.5	29.3	19.53
104	MID	29/5	D3	3/6	4.0	12.5	3.13
105	MID	29/5	E2	3/6	4.0	9.0	2.25
106	MID	29/5	L5	7/6	8.5	29.3	3.45
107	MID	29/5	L3	19/6	20.5	27.5	1.34
109	MID	29/5	A2	31/5	1.5	28.0	18.67
113	MID	3/6	A2	7/6	3.5	28.0	8.00
113	A2	7/6	A4	17/6	9.0	10.0	1.11
113	A4	17/6	A2	3/7	25.5	10.0	0.39
113	A4	3/7	A5	10/7	6.0	5.0	0.83
113	A5	10/7	A4	24/7	13.0	5.0	0.38
115	MID	3/6	G5	10/6	6/0	10.3	1.72
116	MID	3/6	H4	10/6	6.0	9.0	1.50
116	H4	10/6	I2	17/6	6.0	11.2	1.86
117	MID	3/6	J3	19/6	15.5	17.5	1.13
120	MID	3/6	A5	10/7	36.5	29.3	0.80
121	MID	3/6	A5	17/6	13.0	29.3	2.25
122	MID	3/6	J5	26/6	22.5	29.3	1.30
123	MID	3/6	F1	26/6	22.5	10.3	0.46
123	F1	26/6	E1	28/6	1.5	5.0	3.33
125	MID	3/6	J1	26/6	22.5	20.2	0.90
125	J1	26/6	L2	1/7	4.0	11.2	2.80
125	L2	1/7	H3	5/7	3.5	20.6	5.89
126	L1	21/6	A1	28/6	6.5	55.0	8.46
129	MID	3/6	L4	21/6	17.5	28.0	1.60
129	L4	21/6	K3	5/7	13.5	7.1	0.52
130	MID	3/6	L3	26/6	22.5	27.5	1.22

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No	Rel	Date	Rec	Date	Days	Disp	m/day
134	MID	3/6	I1	1/7	27.0	16.0	0.59
137	MID	3/6	A3	5/6	1.5	27.5	18.33
138	MID	3/6	G4	5/6	1.5	5.6	3.73
139	MID	3/6	K1	21/6	17.5	24.6	1.41
140	MID	3/6	J2	26/6	22.5	18.2	0.81
141	MID	3/6	A1	21/6	17.5	29.3	1.67
141	A1	21/6	A1	24/6	2.0	0.0	0.00
141	A1	24/6	A1	26/6	1.5	0.0	0.00
143	MID	3/6	L2	12/6	8.5	28.0	3.29
144	MID	3/6	I4	17/6	13.0	13.5	1.04
145	MID	3/6	H2	17/7	13.0	9.0	0.69
146	MID	3/6	G2	19/6	15.5	5.6	0.36
147	MID	3/6	K5	3.7	1.5	14.1	9.43
148	MID	3/6	G1	5/6	1.5	10.3	6.87
148	G1	5/6	B2	17/6	11.0	24.5	2.23
149	MID	3/6	A5	10/6	6.0	29.3	4.88
149	A5	10/6	A4	21/6	10.5	5.0	0.48
151	MID	3/6	L4	15/7	41.0	28.0	0.68
152	MID	3/6	E1	5/6	1.5	12.5	8.33
155	MID	3/6	L4	17/6	13.0	28.0	2.15
155	L4	17/6	I3	17/7	29.5	15.8	0.54
156	MID	3/6	J4	5/7	31.5	18.2	0.58
157	MID	3/6	E2	15/7	41.0	9.0	0.22
159	MID	3/6	H1	17/6	13.0	12.5	0.96
160	MID	3/6	I1	26/6	22.5	16.0	0.71
2	MID	5/6	B3	12/6	6.5	22.5	3.46
8	MID	5/6	G5	10/6	4.0	10.3	2.58
8	G5	10/6	L2	1/7	20.0	29.5	1.46
10	MID	5/6	G2	17/6	11.0	5.6	0.51
11	MID	5/6	I3	1/7	25.0	12.5	0.50
12	MID	5/6	I3	1/7	25.0	12.5	0.50
21	MID	5/6	K2	8/7	32.0	23.0	0.72
25	MID	5/6	E2	1/7	25.0	9.0	0.36
25	E2	1/7	G3	12/7	10.5	14.1	1.35
25	G3	12/7	I4	17/7	4.5	7.1	1.57
30	MID	5/6	H3	10/6	4.0	7.5	1.88
30	H3	10/6	H2	3/7	22.5	5.0	0.22
32	MID	5/6	F1	1/7	25.0	10.3	0.41
34	MID	5/6	G2	1/7	25.0	5.6	0.22
39	MID	5/6	J4	17/6	11.0	18.2	1.65
40	MID	5/6	B5	17/6	11.0	24.6	2.24
42	MID	5/6	K2/	17/6	11.0	23.0	2.09
43	MID	5/6	K3	24/6	18.0	22.5	1.25
46	MID	5/6	H2	17/7	41.5	9.0	0.22
53	MID	5/6	F3	10/6	4.0	2.5	0.63
53	F3	10/6	G2	19/6	8.5	7.1	0.83
53	G2	19/6	F3	5/7	15.5	7.1	0.83
57	MID	5/6	D5	12/6	6.5	16.0	2.46
57	D5	12/6	E3	17/6	4.0	11.2	2.80
59	MID	5/6	C3	21/6	15.5	17/5	1.13

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No	Rel	Date	Rec	Date	Days	Disp	m/day
134	MID	3/6	I1	1/7	27.0	16.0	0.59
137	MID	3/6	A3	5/6	1.5	27.5	18.33
138	MID	3/6	G4	5/6	1.5	5.6	3.73
139	MID	3/6	K1	21/6	17.5	24.6	1.41
140	MID	3/6	J2	26/6	22.5	18.2	0.81
141	MID	3/6	A1	21/6	17.5	29.3	1.67
141	A1	21/6	A1	24/6	2.0	0.0	0.00
141	A1	24/6	A1	26/6	1.5	0.0	0.00
143	MID	3/6	L2	12/6	8.5	28.0	3.29
144	MID	3/6	I4	17/6	13.0	13.5	1.04
145	MID	3/6	H2	17/7	13.0	9.0	0.69
146	MID	3/6	G2	19/6	15.5	5.6	0.36
147	MID	3/6	K5	3.7	1.5	14.1	9.43
148	MID	3/6	G1	5/6	1.5	10.3	6.87
148	G1	5/6	B2	17/6	11.0	24.5	2.23
149	MID	3/6	A5	10/6	6.0	29.3	4.88
149	A5	10/6	A4	21/6	10.5	5.0	0.48
151	MID	3/6	L4	15/7	41.0	28.0	0.68
152	MID	3/6	E1	5/6	1.5	12.5	8.33
155	MID	3/6	L4	17/6	13.0	28.0	2.15
155	L4	17/6	I3	17/7	29.5	15.8	0.54
156	MID	3/6	J4	5/7	31.5	18.2	0.58
157	MID	3/6	E2	15/7	41.0	9.0	0.22
159	MID	3/6	H1	17/6	13.0	12.5	0.96
160	MID	3/6	I1	26/6	22.5	16.0	0.71
2	MID	5/6	B3	12/6	6.5	22.5	3.46
8	MID	5/6	G5	10/6	4.0	10.3	2.58
8	G5	10/6	L2	1/7	20.0	29.5	1.46
10	MID	5/6	G2	17/6	11.0	5.6	0.51
11	MID	5/6	I3	1/7	25.0	12.5	0.50
12	MID	5/6	I3	1/7	25.0	12.5	0.50
21	MID	5/6	K2	8/7	32.0	23.0	0.72
25	MID	5/6	E2	1/7	25.0	9.0	0.36
25	E2	1/7	G3	12/7	10.5	14.1	1.35
25	G3	12/7	I4	17/7	4.5	7.1	1.57
30	MID	5/6	H3	10/6	4.0	7.5	1.88
30	H3	10/6	H2	3/7	22.5	5.0	0.22
32	MID	5/6	F1	1/7	25.0	10.3	0.41
34	MID	5/6	G2	1/7	25.0	5.6	0.22
39	MID	5/6	J4	17/6	11.0	18.2	1.65
40	MID	5/6	B5	17/6	11.0	24.6	2.24
42	MID	5/6	K2	17/6	11.0	23.0	2.09
43	MID	5/6	K3	24/6	18.0	22.5	1.25
46	MID	5/6	H2	17/7	41.5	9.0	0.22
53	MID	5/6	F3	10/6	4.0	2.5	0.63
53	F3	10/6	G2	19/6	8.5	7.1	0.83
53	G2	19/6	F3	5/7	15.5	7.1	0.83
57	MID	5/6	D5	12/6	6.5	16.0	2.46
57	D5	12/6	E3	17/6	4.0	11.2	2.80
59	MID	5/6	C3	21/6	15.5	17/5	1.13

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No	Rel	Date	Rec	Date	Days	Disp	m/day
60	MID	5/6	E1	10/6	4.0	12.5	3.13
61	MID	5/6	A4	26/6	20.5	28.0	1.37
62	MID	5/6	A5	5/7	29.5	29.3	0.99
63	MID	5/6	H1	14/6	8.5	12.5	1.47
63	H1	14/6	E1	17/6	2.0	15.0	7.50
82	MID	5/6	G3	7/6	1.5	2.5	1.67
82	G3	7/6	H3	12/7	34.5	5.0	0.14
87	MID	5/6	F2	21/6	18.5	5.6	0.30
90	MID	5/6	D5	17/6	11.0	16.0	1.45
108	MID	5/6	G3	7/6	1.5	2.5	1.67
104	MID	5/6	H1	3/7	27.5	12.5	0.45
105	MID	5/6	G3	7/6	1.5	2.5	1.67
105	G3	7/6	F3	17/6	9.0	5.6	0.56
109	MID	5/6	J2	12/6	6.5	5.6	0.86
109	F2	12/6	J2	26/6	9.5	20.0	2.11
161	MID	5/6	I1	7/6	1.5	16.0	10.67
161	I1	7/6	H4	26/6	18.5	15.8	0.85
162	MID	5/6	E1	10/6	4.0	12.5	3.13
163	MID	5/6	I3	8/7	32.0	12.5	0.39
164	MID	5/6	G1	10/6	4.0	10.3	2.58
165	MID	5/6	F3	7/6	1.5	2.5	1.67
167	MID	5/6	L5	12/6	6.5	29.3	4.51
167	L5	12/6	H3	26/6	13.5	22.4	1.66
169	MID	5/6	A1	17/6	11.0	29.3	2.66
170	MID	5/6	L3	1/7	25.0	27.5	1.10
171	MID	5/6	H3	7/6	1.5	7.5	5.00
172	MID	5/6	A5	5/7	29.5	29.3	0.99
174	MID	7/6	A1	26/6	18.5	29.3	1.58
175	MID	7/6	A4	17/6	9.0	28.0	3.11
176	MID	7/6	G3	10/6	2.0	2.5	1.25
176	G3	10/6	I2	1/7	20.0	11.2	0.56
176	I2	1/7	H2	5/7	3.5	5.0	1.43
181	MID	7/6	C2	28/6	20.5	18.2	0.89
181	C2	28/6	C2	1/7	2.0	0.0	0.00
181	C2	1/7	C1	3/7	1.5	5.0	3.33
183	MID	7/6	A4	3/7	25.5	28.0	1.10
184	MID	7/6	E3	17/6	9.0	7.5	0.83
186	MID	7/6	K3	19/6	11.5	22.5	1.96
186	K3	19/6	L2	5/7	15.5	7.1	0.46
187	MID	7/6	G1	24/6	16.0	10.3	0.64
187	G1	24/6	I2	5/7	10.5	11.2	1.06
187	I2	5/7	I3	17/7	11.5	5.0	0.43
191	MID	7/6	J2	1/7	23.0	18.2	0.79
192	MID	7/6	E3	10/6	2.0	7.5	3.75
192	E3	10/6	B1	26/6	15.5	18.0	1.16
194	MID	12/6	L3	5/7	22.5	27.5	1.22
196	MID	12/6	J5	17/6	4.0	20.2	5.05
197	MID	12/6	B4	24/6	11.0	23.0	2.09

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No	Rel	Date	Rec	Date	Days	Disp	m/day
199	MID	12/6	I5	5/8	53.0	16.0	0.30
200	MID	12/6	F2	3/7	20.5	5.6	0.27
200	F2	3/7	G2	5/7	1.5	5.0	3.33
200	G2	5/7	G4	10/7	4.5	10.0	2.22
200	G4	10/7	I2	12/7	1.5	14.1	9.43
200	I2	12/7	H3	15/7	2.0	7.1	3.54
200	H3	15/7	G1	9/8	24.5	11.2	0.46
201	MID	12/6	F1	1/7	18.0	10.3	0.57
204	MID	12/6	B3	17/6	4.0	22.5	5.63
205	MID	12/6	I3	1/7	18.0	12.5	0.69
206	MID	12/6	I3	8/7	25.0	12.5	0.50
210	MID	12/6	A5	5/7	22.5	29.3	1.30
212	MID	12/6	G2	19/6	6.5	5.6	0.86
212	G2	19/6	E1	3/7	13.5	11.2	0.83
214	MID	12/6	E5	24/6	11.0	12.5	1.14
214	E5	24/6	I3	1/7	6.0	22.4	3.73
214	I3	1/7	G2	5/7	3.5	11.2	3.19
215	MID	12/6	I2	24/6	11.0	13.5	1.23
216	MID	12/6	I3	8/7	25.0	12.5	0.50
217	MID	12/6	G2	8/7	25.0	5.6	0.22
218	MID	12/6	A5	19/6	6.5	29.3	4.51
218	A5	19/6	A1	26/6	6.5	20.0	3.08
218	A1	26/6	A5	10/7	13.5	20.0	1.48
218	A5	10/7	B3	15/7	4.0	11.2	2.80
219	MID	12/6	L3	19/6	6.5	27.5	4.23
219	L3	19/6	I2	12/7	22.5	15.8	0.70
220	MID	12/6	D5	26/6	13.5	16.0	1.19
221	MID	12/6	L1	19/6	6.5	29.3	4.51
221	L1	19/6	L3	3/7	13.5	24.6	1.82
223	MID	12/6	K1	17/6	4.0	24.6	6.15
224	MID	12/6	D3	21/6	8.5	12.5	1.47
224	D3	21/6	B4	17/7	25.5	11.2	0.44
225	MID	12/6	A4	14/8	62.5	28.0	0.45
226	MID	12/6	K3	28/6	15.5	22.5	1.45
226	K3	28/6	K3	1/7	2.0	0.0	0.00
226	K3	1/7	K3	3/7	1.5	0.0	0.00
227	MID	12/6	F1	17/6	4.0	10.3	2.58
228	MID	12/6	B5	17/6	4.0	24.6	6.15
230	MID	12/6	G3	26/6	13.5	2.5	0.19
230	G3	26/6	A2	5/7	8.5	30.4	3.58
230	A2	5/7	B4	15/7	9.0	11.2	1.24
230	B4	15/7	A5	31/7	15.5	7.1	0.46
232	MID	12/6	K2	17/6	4.0	23.0	5.75
236	MID	12/6	E3	17/6	4.0	7.5	1.88
238	MID	12/6	G3	14/6	1.5	2.5	1.67
241	MID	12/6	G1	19/6	6.5	10.3	1.58
241	G1	19/6	G1	21/6	1.5	0.0	0.00
242	MID	12/6	I3	17/6	4.0	12.5	3.13

Harpalus rufipes

No	Rel	Date	Rec	Date	Days	Disp	m/day
2	MID	3/6	J1	12/6	8.5	20.2	2.38
11	MID	5/6	K1	19/6	13.5	24.6	1.82
11	K1	19/6	G1	21/6	1.5	20.0	13.33
16	MID	5/6	A4	26/6	20.5	28.0	1.37
17	MID	5/6	L3	7/6	1.5	27.5	18.33
17	L3	7/6	K5	1/7	23.0	11.2	0.49
19	MID	5/6	C5	17/6	11.0	20.2	1.84
31	MID	5/6	K1	24/6	18.0	24.6	1.37
36	MID	5/6	K5	26/6	20.5	24.6	1.37
36	K5	26/6	F5	5/7	8.5	25.0	2.94
38	MID	5/6	G2	21/6	18.5	5.6	0.30
39	MID	5/6	D5	5/7	29.5	16.0	0.54
50	MID	7/6	L5	17/6	9.0	29.3	3.26
60	MID	7/6	A5	21/6	13.5	29.3	2.17
61	MID	7/6	A5	19/6	11.5	29.3	2.55
61	A5	19/6	A4	23/8	64.5	5.0	0.08
72	MID	7/6	A3	3/7	25.5	27.5	1.08
73	MID	7/6	L2	24/6	16.0	28.0	1.75
77	MID	7/6	K5	1/7	23.0	24.6	1.07
86	MID	7/6	A1	19/6	11.5	29.3	2.55
88	MID	26/6	L1	1/7	4.0	29.3	7.33
92	MID	26/6	L2	1/7	4.0	28.0	7.00
92	L2	1/7	L1	3/7	1.5	5.0	3.33
92	F5	17/7	F5	19/7	1.5	0.0	0.00
113	MID	26/6	B5	3/7	6.5	24.6	3.78
115	MID	26/6	G3	1/7	4.0	2.5	0.63
119	MID	26/6	A1	8/7	11.0	29.3	2.66
124	MID	26/6	L3	3/7	6.5	27.5	4.23
126	MID	26/6	K2	8/7	11.0	23.0	2.09
148	MID	10/7	I2	31/7	20.5	13.5	0.66
151	MID	10/7	L1	12/7	1.5	29.3	19.53
161	MID	10/7	F5	2/8	22.5	10.3	0.46
166	MID	10/7	F2	17/7	6.5	5.6	0.86
173	MID	10/7	F5	2/8	22.5	10.3	0.46
176	MID	10/7	K5	12/8	32.0	24.6	0.77
180	MID	10/7	E2	17/7	6.5	9.0	1.38
190	MID	5/8	D1	12/8	6.0	16.0	2.29
193	MID	5/8	L3	12/8	6.5	27.5	4.58
194	MID	5/8	F5	12/8	6.0	10.3	1.72
195	MID	5/8	L5	9/8	3.5	29.3	8.37
200	MID	5/8	L5	14/8	8.5	29.3	3.45
214	MID	5/8	L3	16/8	10.5	27.5	2.62

Appendix 3

Results of the night tracking

Over the following pages the complete list of each step and turn of each of the tracked beetles is presented.

P. melanarius, Track 1

Step	Bearing
6.0	182.0
0.0	0.0
0.0	0.0
5.0	180.0
12.0	255.0
26.0	272.0
0.0	0.0
0.0	0.0
0.0	0.0
22.0	2.0
48.0	190.0
16.0	152.0
56.0	158.0
52.0	136.0
55.0	344.0
63.0	250.0
23.0	230.0
42.0	76.0
71.0	180.0
18.0	236.0
81.0	68.0
62.0	6.0
83.0	158.0
33.0	103.0
6.0	63.0
0.0	0.0
22.0	150.0
37.0	132.0
119.0	120.0
20.0	153.0
13.0	237.0
36.0	27.0
44.0	4.0
38.0	140.0
17.0	165.0
22.0	242.0
16.0	146.0
117.0	40.0
47.0	31.0
63.0	7.0
17.0	229.0
7.0	178.0
3.0	3.0
68.0	38.0
49.0	64.0
42.0	0.0
63.0	80.0
4.0	125.0
5.0	208.0
25.0	310.0
43.0	195.0
70.0	262.0
63.0	168.0
70.0	358.0

```
                        63.0      232.0
                        86.0      236.0
                        10.0      274.0
                        20.0      122.0
                        31.0        0.0
                        59.0      266.0
                         8.0       19.0
                        31.0      228.0
                        92.0      170.0
                        21.0      151.0
                        36.0       78.0
                        50.0      216.0
                        24.0      201.0
                        31.0      142.0
                        14.0      150.0
            TOTAL DIST. (cm)=    2496.0
            MEAN STEP (cm)=        39.6
            MEAN TURN=                  77.0
```

P. melanarius, Track2

```
                Step        Bearing

                16.0         60.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                12.0         10.0
                71.0         19.0
                85.0         26.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                66.0        200.0
                32.0         14.0
                 0.0          0.0
                17.0         28.0
                32.0         20.0
                27.0        332.0
                47.0         34.0
                22.0         40.0
                24.0        231.0
                31.0        322.0
               170.0        190.0
               125.0        257.0
                15.0        150.0
                31.0        119.0
                60.0        273.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
                 0.0          0.0
```

```
                  3.0      112.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                  4.0       80.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                  0.0        0.0
                 16.0       46.0
                 58.0      136.0
          TOTAL DIST. (cm)=      964.0
          MEAN STEP (cm)=        43.8
          MEAN TURN=                77.1
```

P. melanarius, Track 3

```
             Step      Bearing
              0.0        0.0
              0.0        0.0
              0.0        0.0
              0.0        0.0
             38.0      310.0
             35.0      284.0
              3.0       69.0
             34.0      109.0
             20.0      275.0
             10.0      319.0
             33.0       74.0
             12.0       94.0
              7.0      355.0
              0.0        0.0
             29.0      332.0
              3.0      144.0
             10.0      150.0
             10.0      327.0
             29.0      111.0
             28.0      146.0
             19.0      213.0
             80.0      387.0
             10.0      167.0
             11.0      315.0
             11.0      115.0
             41.0       80.0
             17.0       35.0
              7.0      350.0
             12.0      351.0
             65.0      174.0
             42.0      291.0
              7.0       20.0
             28.0      298.0
```

```
           25.0      332.0
            0.0        0.0
           45.0      275.0
           13.0      215.0
            0.0        0.0
            0.0        0.0
            3.0      359.0
           19.0      354.0
     TOTAL DIST. (cm)=      756.0
     MEAN STEP (cm)=       22.9
     MEAN TURN=                86.1
```

P. melanarius, Track 4

```
        Step       Bearing
       109.0        180.0
        23.0        134.0
         0.0         0.0
        69.0        202.0
         0.0         0.0
         0.0         0.0
         0.0         0.0
         0.0         0.0
        40.0        198.0
        49.0        300.0
        63.0         80.0
         0.0         0.0
        22.0        197.0
        58.0        200.0
        24.0        242.0
        60.0         14.0
        58.0         46.0
        11.0        213.0
        42.0        336.0
        40.0        154.0
        13.0        218.0
        43.0        270.0
        91.0        342.0
        15.0         28.0
         0.0         0.0
         9.0        237.0
         0.0         0.0
         0.0         0.0
         0.0         0.0
        13.0        100.0
        64.0        154.0
         8.0        324.0
         0.0         0.0
        19.0        256.0
        43.0        348.0
        22.0        284.0
        19.0        291.0
        58.0        356.0
         8.0        258.0
        11.0        146.0
        56.0         45.0
        13.0         86.0
```

```
                       20.0      102.0
                        7.0      300.0
                       17.0      147.0
                       37.0      222.0
                        7.0      101.0
                        5.0      127.0
                       16.0      271.0
                       38.0      195.0
                       41.0      204.0
                       23.0      308.0
                        0.0        0.0
                       14.0      214.0
                        9.0       10.0
                        0.0        0.0
                        0.0        0.0
                        0.0        0.0
                        0.0        0.0
             TOTAL DIST. (cm)=    1407.0
             MEAN STEP (cm)=        32.7
             MEAN TURN=                    87.7
```

P. melanarius, Track 5

```
                       Step      Bearing
                       16.0      203.0
                        7.0      220.0
                       38.0      161.0
                       63.0      140.0
                       34.0      270.0
                        3.0       90.0
                        0.0        0.0
                        0.0        0.0
                        0.0        0.0
                        0.0        0.0
                        0.0        0.0
                        4.0      231.0
                        0.0        0.0
                       37.0       64.0
                       39.0       43.0
                       39.0       30.0
                        9.0       51.0
                       21.0      290.0
                       64.0       79.0
                       24.0      120.0
                       22.0      320.0
                        4.0      290.0
                        0.0        0.0
                       44.0       13.0
                       44.0       63.0
                       14.0       73.0
                        7.0      204.0
                       15.0       83.0
                       34.0       82.0
                       38.0       57.0
                       21.0       93.0
                       38.0       50.0
                       54.0        6.0
                       51.0      120.0
                      100.0      123.0
```

99.0	24.0
16.0	144.0
106.0	276.0
29.0	135.0
77.0	60.0
11.0	247.0
41.0	196.0
39.0	12.0
96.0	164.0
26.0	348.0
22.0	1.0
16.0	78.0
7.0	170.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0

```
TOTAL DIST. (cm)=    1469.0
MEAN STEP (cm)=      35.8
MEAN TURN=               85.2
```

H. rufipes, Track 1

Step	Bearing
27.0	56.0
26.0	175.0
30.0	306.0
42.0	42.0
52.0	250.0
37.0	114.0
49.0	90.0
37.0	122.0
12.0	320.0
38.0	142.0
0.0	0.0
0.0	0.0
16.0	136.0
14.0	295.0
12.0	326.0
37.0	125.0
10.0	278.0
13.0	108.0
10.0	60.0
14.0	164.0
15.0	331.0
12.0	1.0
16.0	138.0

```
               0.0        0.0
               7.0      125.0
              12.0      327.0
              22.0      246.0
              15.0      284.0
              59.0      118.0
              19.0      286.0
               9.0       50.0
              29.0       36.0
              34.0       44.0
               0.0        0.0
              28.0       76.0
              26.0      303.0
              41.0      142.0
              35.0       32.0
              25.0      270.0
              25.0       25.0
               0.0        0.0
               0.0        0.0
               6.0       43.0
              11.0      286.0
               0.0        0.0
              28.0      166.0
              12.0      102.0
              13.0      212.0
              40.0      318.0
              18.0      210.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
    TOTAL DIST. (cm)=    1033.0
    MEAN STEP (cm)=       24.0
    MEAN TURN=           101.9
```

H. rufipes, Track 2

```
              Step      Bearing
               6.0       40.0
               0.0        0.0
               3.0       30.0
               0.0        0.0
               9.0      328.0
              26.0      131.0
              77.0      262.0
               7.0       30.0
               2.0      242.0
               0.0        0.0
               2.0       62.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
               0.0        0.0
```

```
64.0     188.0
57.0     256.0
108.0    216.0
20.0     204.0
11.0      32.0
0.0       0.0
11.0     346.0
30.0      30.0
8.0       25.0
0.0       0.0
0.0       0.0
0.0       0.0
19.0     271.0
0.0       0.0
6.0       44.0
25.0     206.0
27.0      44.0
9.0     144.0
20.0     138.0
16.0      91.0
3.0     180.0
0.0       0.0
0.0       0.0
0.0       0.0
39.0     274.0
2.0     224.0
0.0       0.0
0.0       0.0
0.0       0.0
10.0      17.0
15.0     286.0
0.0       0.0
0.0       0.0
0.0       0.0
```

TOTAL DIST. (cm)=   632.0
MEAN STEP (cm)=   22.6
MEAN TURN=   93.9

H. rufipes, Track 3

Step	Bearing
36.0	153.0
199.0	90.0
48.0	81.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
15.0	240.0
9.0	354.0
13.0	200.0
20.0	356.0
26.0	248.0
13.0	73.0
5.0	312.0
7.0	99.0

- A23 -

8.0	70.0
6.0	21.0
0.0	0.0
0.0	0.0
0.0	0.0
7.0	2.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0
14.0	27.0
8.0	30.0
10.0	177.0
0.0	0.0
7.0	340.0
9.0	274.0
12.0	296.0
0.0	0.0
10.0	40.0
34.0	167.0
5.0	288.0
0.0	0.0
0.0	0.0
0.0	0.0
0.0	0.0

```
TOTAL DIST. (cm)=    521.0
MEAN STEP (cm)=      22.7
MEAN TURN=                94.6
```

H. rufipes, Track 4

Step	Bearing
30.0	188.0
11.0	172.0
96.0	94.0
0.0	0.0
1.0	276.0
15.0	179.0
40.0	226.0
0.0	0.0
72.0	100.0
154.0	174.0
0.0	0.0
45.0	120.0
10.0	150.0
0.0	0.0
10.0	38.0
70.0	354.0
50.0	348.0
88.0	56.0
54.0	310.0
115.0	40.0
0.0	0.0
0.0	0.0

```
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                    76.0        226.0
                     9.0        240.0
            TOTAL DIST. (cm)=        946.0
            MEAN STEP (cm)=       52.6
            MEAN TURN=                 77.3
```

H. rufipes, Track 5

```
                    Step        Bearing
                    17.0        295.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                    20.0        110.0
                     0.0          0.0
                     3.0          1.0
                    14.0        190.0
                     0.0          0.0
                     0.0          0.0
                     8.0          6.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     9.0        192.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                    42.0        330.0
                    51.0        358.0
                     5.0         34.0
                     4.0        310.0
                    26.0        294.0
                    28.0        106.0
                    73.0         23.0
                    46.0        332.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                    83.0         54.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
                     0.0          0.0
            TOTAL DIST. (cm)=        429.0
            MEAN STEP (cm)=       28.6
            MEAN TURN=                106.8
```

Appendix 4

Complete listing of the model

The model, for Staddon Heights 1985, presented here contains most

of the features mentioned in Section 7. In particular it contains the

orientation mechanism and the delay effect. In this version each

beetle is treated separately, though in others they all moved

simultaneously.

```
      .top.
C *** PROGRAM TO SIMULATE BEETLE DISPERSAL
C *** By Simon                                    ***
C *** This edition includes delay and orientation  **
      PARAMETER (PI=3.1415926523)
C *** XTRAP & YTRAP CONTAIN CO-ORDINATES OF PITFALLS
      REAL*8 XTRAP(5),YTRAP(6)
C *** ISTATE CONTAINS THE DISPERSAL INDICES
      INTEGER ISTATE(6,5),NP,NST,IZONE1,IPAR,IPAR2
C *** ARRAYS FOR TOTALS AND % IN ZONES AND TRAPS
      REAL TZONE(6,5),PCZONE(6,5),TTRAP(6,5),TIPAR(5)
      REAL AREA(5,4),MAREA(5,4),AAREA(5,4)
C *** MZONE AND AZONE CONTAIN STEP AND TURN IN PATCHES ***
      MZONE(5), AZONE(5)
C *** RANG1 & 2 ARE THE LIMITS OF THE TURN
C *** RDIST1 & 2 ARE THE LIMITS OF THE STEP LENGTH
C *** XS & XF, YS & YF ARE THE CO-ORDINATES OF START & FINISH
C *** MOVE IS THE STEP LENGTH
      REAL*8 RANG1,RANG2,RDIST1,RDIST2,XS,XF,YS,YF,MOVE
C *** ALPHA IS THE ANGLE OF TURN
C *** DIRN IS THE BEARING
      REAL ALPHA,DIRN,PARM(5,2,5),PART(5,2,5),VAL(2,5),VALT(2,5)
C *** TX,TY,GX,GY ARE CO-OODS OF TRAPS WHEN CAUGHT ***
      REAL*8 TX,TY,GX,GY
C *** PARM HAS THE LIMITS OF THE STEPS
C *** PART HAS THE LIMITS OF THE TURNS
      COMMON/VALUES/PART,PARM,VAL,VALT
*
      READ(5,*)(((PARM(I,J,K),K=1,5),J=1,2),I=1,5)
      READ(5,*)(((PART(I,J,K),K=1,5),J=1,2),I=1,5)
*
C *** PATCH INDICES ***
      DATA ((ISTATE(I,J),J=1,2),I=1,6)/1,5,2,4,2,2,3,3,4,5,2,4/
      DATA ((ISTATE(I,J),J=3,4),I=1,6)/5,4,5,1,5,5,1,4,3,2,2,1/
      DATA (ISTATE(I,5),I=1,6)/3,2,1,4,4,3/
*
      DATA TZONE/30*0/,AREA/20*0/,MAREA/20*0/,AAREA/20*0/
      DATA TIPAR/5*0/,MZONE/5*0/,AZONE/5*0/
      DATA TTRAP/30*0/
*
C *** COORDINATES OF TRAPS ***
      DATA (XTRAP(I),I=1,5)/0,1000,2000,3000,4000/
      DATA (YTRAP(I),I=1,6)/0,1000,2000,3000,4000,5000/
*
C *** XG & YG ARE THE CO-ORDINATES OF THE GUTTERS
      XG=-2000
      YG=-2000
*
      NO=0
      TOTALL=0
*
C *** INITIALISE NAG ROUTINES ***
      CALL G05CCF
*
      TMOVE=0.0
      TANG=0.0
      TDISP=0.0
```

```
        TDISP=0.0
*
C *** START FOR INDIVIDUAL BEETLES ***
        DO 5 L=1,100
        IDELAY=10
        NO=NO+1
        NP=0
        IDAY=0
        TDIST=0.0
        DIRN=G05DYF(1,360)*PI/180
C *** SET INITIAL BEARING ***
        TALPHA=0.0
        N=0
        K2=1
        IR=1
C *** SET START POSITION ***
        XS=2000
        YS=2500
*
C *** SET NUMBER OF DAYS ***
        WHILE (K2.LE.35) DO
        IDAY=IDAY+1
        K=1
*
C *** MOVE FOR 1 DAY (240 STEPS) ***
        WHILE (K.LE.240) DO
         IX=0
         IY=0
         IDIFFX=0
         IDIFFY=0
         ITX=0
         ITY=0
        NP=0
        IDELAY=IDELAY+1
        IR=IR+1
*
C *** SET DISPERSAL INDEX IN AREAS OUTSIDE GRID ***
        IPAR=3
        IF(XS.LT.-500.AND.XS.GE.-2000.AND.
       1YS.GE.-500.AND.YS.LE.5500) THEN
        IPAR=1
        ENDIF
*
C *** SET DISPERSAL INDEX WITHIN PATCHES OF GRID ***
        IF (XS.GE.-500.AND.XS.LE.4500.AND.
       1YS.GE.-500.AND.YS.LE.5500) THEN
*
          DO 10 I=-500,3500,1000
            DO 15 J=-500,4500,1000
              IF (XS.GE.I.AND.XS.LE.(I+1000)) THEN
               IF (YS.GE.J.AND.YS.LE.(J+1000)) THEN
               IST=(I+1500)/1000
               IJST=(J+1500)/1000
               IZONE=ISTATE(IJST,IST)
               IPAR=IZONE
               TZONE(IJST,IST)=TZONE(IJST,IST)+1
               TOTALL=TOTALL+1
```

```
                TOTALL=TOTALL+1
            IF (K.EQ.1.AND.K2.EQ.1) THEN
            IPAR2=IZONE
            IZONE1=IZONE
            ENDIF
*
C *** SET DELAY IF PATCHES DIFFERENT ***
            IF (IZONE1.NE.IZONE) THEN
            IDELAY=1
            ENDIF
*
C *** DECIDE THE ZONE WITHIN A PATCH ***
            XD=(I+500)-XS
            YD=(J+500)-YS
*
            XDIST=ABS((I+500)-XS)
            YDIST=ABS((J+500)-YS)
*
             IF (XDIST.LE.250) THEN
*
              IF (YDIST.LE.250) THEN
               AREA(IZONE,1)=AREA(IZONE,1)+1
               IA=1
              ELSE IF (YDIST.GT.250.AND.YDIST.LE.354) THEN
               AREA(IZONE,2)=AREA(IZONE,2)+1
               IA=2
              ELSE IF (YDIST.GT.354.AND.YDIST.LE.433) THEN
               AREA(IZONE,3)=AREA(IZONE,3)+1
               IA=3
              ELSE
               AREA(IZONE,4)=AREA(IZONE,4)+1
               IA=4
              ENDIF
*
             ELSE IF (XDIST.GT.250.AND.XDIST.LE.354) THEN
*
              IF (YDIST.LE.354) THEN
               AREA(IZONE,2)=AREA(IZONE,2)+1
               IA=2
              ELSE IF (YDIST.GT.354.AND.YDIST.LE.433) THEN
               AREA(IZONE,3)=AREA(IZONE,3)+1
               IA=3
              ELSE
               AREA(IZONE,4)=AREA(IZONE,4)+1
               IA=4
              ENDIF
*
             ELSE IF (XDIST.GT.354.AND.XDIST.LE.433) THEN
*
              IF (YDIST.LE.433) THEN
               AREA(IZONE,3)=AREA(IZONE,3)+1
               IA=3
              ELSE
               AREA(IZONE,4)=AREA(IZONE,4)+1
               IA=4
              ENDIF
*
```

```
              IA=4
            ENDIF
*
            ELSE IF (XD.GT.433) THEN
              AREA(IZONE,4)=AREA(IZONE,4)+1
              IA=4
            ENDIF
*
          ENDIF
        ENDIF
*
15      CONTINUE
10      CONTINUE
*
      ENDIF
*
C *** IF DELAY IN EFFECT SET EARLIER IPAR VALUE ***
      IF (IDELAY.LE.2) THEN
        IPAR=IPAR2
      ENDIF
*
C *** SET STEP AND TURN SIZE ***
      CALL RANGEN(RDIST1,RDIST2,RANG1,RANG2,K1,IPAR)
      ALPHA=G05DAF(RANG1,RANG2)
      MOVE=G05DAF(RDIST1,RDIST2)
*
      IF (XS.GE.-500.AND.XS.LE.4500) THEN
        IF (YS.GE.-500.AND.YS.LE.5500) THEN
          MZONE(IZONE)=MZONE(IZONE)+MOVE
          AZONE(IZONE)=AZONE(IZONE)+((ALPHA/PI)*180)
          MAREA(IZONE,IA)=MAREA(IZONE,IA)+MOVE
          AAREA(IZONE,IA)=AAREA(IZONE,IA)+((ALPHA/PI)*180)
          TIPAR(IZONE)=TIPAR(IZONE)+1
*
          IF (IR.GE.0) THEN
C *** CHECK TO SEE WHETHER IT WILL RESPOND
C     TO ORIENTATION MECHANISM ***
            IRESP=G05DYF(1,100)
            IF (IRESP.GE.90) THEN
              IR=-10
            ENDIF
          ENDIF
*
        ENDIF
      ENDIF
*
      TDIST=TDIST+MOVE
      DIRN=DIRN+K1*ALPHA
*
      IF (IR.GE.0) THEN
C *** THE NEXT SECTION CHECKS DIFFERENCE BETWEEN
C     TWO PATCHES, AND STARTS ORIENTATION ***
*
      IF (XD.LE.-350) THEN
        ORX=PI
        IST2=IST-1
        IX=1
```

```
         IX=1
        ELSE IF (XD.GE.350) THEN
         ORX=0
         IST2=IST+1
         IX=1
        ENDIF
*
        IF (YD.LE.-350) THEN
         ORY=3*PI/2
         IJST2=IJST+1
         IY=1
        ELSE IF (YD.GE.350) THEN
         ORY=PI/2
         IJST2=IJST-1
         IY=1
        ENDIF
*
        IF (IST2.GE.1.AND.IST2.LE.5) THEN
         IF (IX.GT.0) THEN
          IDIFFX=IZONE-ISTATE(IJST,IST2)
         ENDIF
        ENDIF
*
        IF (IJST2.GE.1.AND.IJST2.LE.6) THEN
         IF (IY.GT.0) THEN
          IDIFFY=IZONE-ISTATE(IJST2,IST)
         ENDIF
        ENDIF
*
        IF (IST2.EQ.0) THEN
         IF (IX.GT.0) THEN
         IDIFFX=IZONE-1
         ENDIF
        ELSE IF (IST2.EQ.6) THEN
         IF (IX.GT.0) THEN
         IDIFFX=IZONE-3
         ENDIF
        ENDIF
*
        IF (IJST2.EQ.0.OR.IJST2.EQ.7) THEN
         IF (IY.GT.0) THEN
         IDIFFY=IZONE-3
         ENDIF
        ENDIF
*
        IPROR=G05DYF(1,100)
*
        IF (IX.GT.0) THEN
         IF (IDIFFX.LT.0) THEN
           IF (IPROR.LE.(IDIFFX*20)) THEN
            DIRN=ORX
            ITX=1
           ENDIF                        .
          ENDIF
         ENDIF
*
        ELSE IF (IY.GT.0) THEN
         IF (IDIFFY.LT.0) THEN
```

```
            IF (IDIFFY.LT.0) THEN
               IF (IPROR.LE.(IDIFFY*20)) THEN
               DIRN=ORY
               ITY=1
               ENDIF
            ENDIF

         ELSE IF (IX.GT.0.AND.IY.GT.0) THEN
          IF (IDIFFX.LT.0.AND.IDIFFY.LT.0) THEN
           IF (IDIFFX.GT.IDIFFY) THEN
             IF (ITX.GT.0) THEN
             DIRN=ORX
             ENDIF
           ELSE IF (IDIFFY.GT.IDIFFX) THEN
             DIRN=ORY
             ENDIF
           ELSE IF (IDIFFX.EQ.IDIFFY) THEN
             ICHOO=G05DYF(1,2)
             IF (ICHOO.EQ.1.AND.ITX.GT.0) THEN
             DIRN=ORX
             ELSE IF (ICHOO.EQ.2.AND.ITY.GT.0) THEN
             DIRN=ORY
             ENDIF
           ENDIF
          ENDIF
```
```
         ENDIF
```
```
C *** MOVE BEETLE ***
         XF=XS+(MOVE*COS(DIRN))
         YF=YS+(MOVE*SIN(DIRN))
         ALPHA=(ALPHA/PI)*180
C
C *** CHECK WHETHER IT IS NEAR A PITFALL ***
         IF(MOVE.GT.0.001) THEN
      N=N+1
      TALPHA=TALPHA+ABS(ALPHA)
      NST=0
         DO 20 I=1,5
         DO 30 J=1,6
```
```
            CALL CHECK(XS,XF,YS,YF,XTRAP(I),YTRAP(J),TX,TY,NP,N)
            IF (NP.GT.0.AND.NST.EQ.0) THEN
             TTRAP(J,I)=TTRAP(J,I)+1
             NST=1
             ENDIF
```
```
30       CONTINUE
20       CONTINUE
```
```
C *** CHECK WHETHER IT IS NEAR A GUTTER ***
         IF(XS.LE.-1800.AND.XS.GE.-2200) THEN
          IF(XS.GT.XF) THEN
           IF (XS.GE.(XG+5).AND.XF.LE.(XG+5)) THEN
           NG=1
           CALL GUTTER(XS,XF,YS,YF,GX,GY,NP,NG)
           ENDIF
```

```
            ENDIF
           ELSE IF(XS.LT.XF) THEN
            IF (XS.LE.(XG-5).AND.XF.GE.(XG-5)) THEN
            NG=1
            CALL GUTTER(XS,XF,YS,YF,GX,GY,NP,NG)
            ENDIF
           ENDIF
          ENDIF
*
          IF (YS.LE.-1800.AND.YS.GE.-2200) THEN
           IF(YS.GT.YF) THEN
            IF(YS.GE.(YG+5).AND.YF.LE.(YG+5)) THEN
            NG=2
            CALL GUTTER(XS,XF,YS,YF,GX,GY,NP,NG)
            ENDIF
           ELSE IF(YS.LT.YF) THEN
            IF(YS.LE.(YG-5).AND.YF.GE.(YG-5)) THEN
            NG=2
            CALL GUTTER(XS,XF,YS,YF,GX,GY,NP,NG)
            ENDIF
           ENDIF
          ENDIF
*
         ENDIF
*
C *** SET NEW START POSITION ***
          XS=XF
          YS=YF
          IZONE1=IZONE
*
C *** IF BEETLE HAS MOVED INTO TRAP CHECK
C     IT IS TRAPPED ***
          IF (NP.GT.0) THEN
           ITRAP=G05DYF(1,100)
           IF (NP.LE.5) THEN
            IF (ITRAP.LE.75) THEN
             K=2000
             K2=1000
             XF=TX
             YF=TY
            ENDIF
           ELSE IF (NP.EQ.6) THEN
            IF (ITRAP.LE.90) THEN
             K=2000
             K2=1000
             XF=GX
             YF=GY
            ENDIF
           ENDIF
          ENDIF
*
          IF (IDELAY.LE.2) THEN
           IPAR2=IPAR
          ELSE
           IPAR2=IZONE
          ENDIF
           K=K+1
```

```
          K=K+1
          ENDWHILE
  *
          K2=K2+1
          ENDWHILE
  *
C *** CALCULATE DISPLACEMENT ***
          DISP=SQRT(((XF-2000)**2)+((YF-2500)**2))
          TANG=TANG+TALPHA/N
          TMOVE=TMOVE+TDIST/N
          TDISP=TDISP+DISP/100
          DD=(DISP/100)/IDAY
C *** PRINT DATA FOR INDIVIDUAL ***
          WRITE(6,500)NO,NP,XF,YF,TDIST,TDIST/N,
     1 TALPHA/N,DISP/100,N,IDAY,DD
  500     FORMAT(2I4,2F8.0,F9.0,3F7.1,2I5,F6.2)
  5       CONTINUE
  *
C *** PRINT MEAN FOR ALL INDIVIDUALS ***
          WRITE(6,510)TDISP/(L-1),TMOVE/(L-1),TANG/(L-1)
  510     FORMAT('MEAN DISPERSAL',F8.2/,'MEAN STEP',F8.2/,'MEAN TURN',F8.2)
          WRITE(6,520)
  520     FORMAT(//'TOTAL FOR EACH ZONE',//)
          WRITE(6,530)((TZONE(I,J),J=1,5),I=1,6)
  530     FORMAT(5F10.0)
          WRITE(6,540)TOTALL
  540     FORMAT(/,'TOTAL OF ALL TRAPS=',F12.0,/)
          WRITE(6,550)
  550     FORMAT(//'TOTAL IN EACH TRAP',//)
          WRITE(6,560)((TTRAP(I,J),J=1,5),I=1,6)
  560     FORMAT(5F6.0)
          DO 80 J=1,6
           DO 90 I=1,5
           PCZONE(J,I)=TZONE(J,I)*100/TOTALL
           IF (TTRAP(J,I).GT.0.000001) THEN
           TTRAP(J,I)=TTRAP(J,I)*10000/TZONE(J,I)
           ENDIF
  90       CONTINUE
  80       CONTINUE
          WRITE(6,570)
  570     FORMAT(/,'PERCENTAGES IN EACH ZONE',/)
          WRITE(6,580)((PCZONE(I,J),J=1,5),I=1,6)
  580     FORMAT(5F6.2)
          WRITE(6,590)
  590     FORMAT(/,'TRAPPING INDEX FOR EACH TRAPS',/)
          WRITE(6,600)((TTRAP(I,J),J=1,5),I=1,6)
  600     FORMAT(5F6.2)
          DO 100 I=1,5
          IF (TIPAR(I).GT.0.001) THEN
           MZONE(I)=MZONE(I)/TIPAR(I)
           AZONE(I)=AZONE(I)/TIPAR(I)
          ENDIF
  100     CONTINUE
          WRITE(6,610)
  610     FORMAT(///'MEAN STEP AND TURN IN EACH AREA',//)
          WRITE(6,620)(MZONE(I),I=1,5)
  620     FORMAT(5F8.1)
```

```
620     FORMAT(5F8.1)
        WRITE(6,630)(AZONE(I),I=1,5)
630     FORMAT(5F8.1)
        WRITE(6,640)
640     FORMAT(//,'TOTALS IN EACH SUBZONE',//)
        WRITE(6,650)((AREA(I,J),J=1,4),I=1,5)
650     FORMAT(4F9.0)
        DO 91 I=1,5
         DO 92 J=1,4
         IF (AREA(I,J).GT.0.1) THEN
         MAREA(I,J)=MAREA(I,J)/AREA(I,J)
         AAREA(I,J)=AAREA(I,J)/AREA(I,J)
         ENDIF
92       CONTINUE
91      CONTINUE
        WRITE(6,660)
660     FORMAT(/,'MEAN STEP AND TURN IN EACH SUBZONE',//)
        WRITE(6,670)((MAREA(I,J),J=1,4),I=1,5)
        WRITE(6,670)((AAREA(I,J),J=1,4),I=1,5)
670     FORMAT(4F8.1)
        STOP
    .   END
*
        BLOCK DATA
C ***   THIS SECTION SETS LIMITS OF STPES AND TURNS ***
        REAL PART(5,2,5),PARM(5,2,5),VAL(2,5),VALT(2,5)
        COMMON/VALUES/PART,PARM,VAL,VALT
        DATA (VAL(1,I),I=1,5)/0,1,21,41,71/
        DATA (VAL(2,I),I=1,5)/0,20,40,70,150/
        DATA (VALT(1,I),I=1,5)/0,21,41,121,141/
        DATA (VALT(2,I),I=1,5)/20,40,120,140,180/
        END
*
C       ROUTINE TO PRODUCE DIRECTION AND DISTANCE MOVED
        SUBROUTINE RANGEN(RDIST1,RDIST2,RANG1,RANG2,K1,IP)
        REAL*8 RDIST1,RDIST2
        REAL*8 RANG1,RANG2
        INTEGER*2 RAN1,RAN2
        REAL PART(5,2,5),PARM(5,2,5),VAL(2,5),VALT(2,5)
        PARAMETER (PI=3.1415926523)
        COMMON/VALUES/PART,PARM,VAL,VALT
*
C   **** POSITIVE OR NEGATIVE TURN ****
*
        K1=G05DYF(0,1)
*
        IF (K1.EQ.0) THEN
        K1=-1
        ELSE
        K1=1
        ENDIF
*
        RAN1=G05DYF(0,100)          .
        DO 10 I=1,5
        IF (RAN1.GE.PARM(IP,1,I).AND.RAN1.LT.PARM(IP,2,I)) THEN
        RDIST1=VAL(1,I)
        RDIST2=VAL(2,I)
```

```
          RDIST2=VAL(2,I)
          ENDIF
 10       CONTINUE
 *
          RAN2=G05DYF(0,100)
          DO 20 I=1,5
          IF (RAN2.GE.PART(IP,1,I).AND.RAN2.LT.PART(IP,2,I)) THEN
          RANG1=VALT(1,I)*PI/180
          RANG2=VALT(2,I)*PI/180
          ENDIF
 20       CONTINUE
 *
          RETURN
          END
C *** A SUBROUTINE TO SEE IF THERE ARE ANY TRAPS AROUND
          SUBROUTINE CHECK(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
          REAL*8 XS,XF,YS,YF,XT,YT,TX,TY
 *
            IF(XS.LE.XF.AND.YS.LE.YF) THEN
              IF (XS.LE.XT.AND.XF.GE.XT
     1        .AND.YS.LE.YT.AND.YF.GE.YT) THEN
              CALL CATCH(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
              ENDIF
 *
            ELSE IF (XS.GE.XF.AND.YS.LE.YF) THEN
              IF (XS.GE.XT.AND.XF.LE.XT
     1        .AND.YS.LE.YT.AND.YF.GE.YT) THEN
              CALL CATCH(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
              ENDIF
 *
            ELSE IF (XS.LE.XF.AND.YS.GE.YF) THEN
              IF(XS.LE.XT.AND.XF.GE.XT
     1        .AND.YS.GE.YT.AND.YF.LE.YT) THEN
              CALL CATCH(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
              ENDIF
 *
            ELSE IF (XS.GE.XF.AND.YS.GE.YF) THEN
              IF (XS.GE.XT.AND.XF.LE.XT
     1        .AND.YS.GE.YT.AND.YF.LE.YT) THEN
              CALL CATCH(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
              ENDIF
 *
            ENDIF
 *
          RETURN
          END
C *** SUBROUTINE TO CALCULATE IF THE BEETLE IS CAUGHT
          SUBROUTINE CATCH(XS,XF,YS,YF,XT,YT,TX,TY,NP,N)
          REAL*8 XS,XF,YS,YF,XT,YT,TX,TY
          REAL M
            IF (XF.EQ.XS) THEN
              IF (YS.LE.YF) THEN
                IF(YT.GE.YS.AND.YT.LE.YF) THEN
                  IF(ABS(XS-XT).LE.4.5) THEN
                  TX=XT
                  TY=YT
                  NP=1                      - A36 -
```

```
            NP=1
           ENDIF
          ENDIF
         ELSE IF(YS.GE.YF) THEN
          IF(YT.LE.YS.AND.YT.GE.YF) THEN
            IF(ABS(XS-XT).LE.4.5) THEN
            TX=XT
            TY=YT
            NP=2
            ENDIF
          ENDIF
         ENDIF
        ELSE IF (YF.EQ.YS) THEN
         IF(XS.LE.XF) THEN
          IF(XT.GE.XS.AND.XT.LE.XF) THEN
            IF(ABS(YS-YT).LE.4.5) THEN
            TX=XT
            TY=YT
            NP=3
            ENDIF
          ENDIF
         ELSE IF(XS.GE.XF) THEN
          IF(XT.LE.XS.AND.XT.GE.XF) THEN
            IF(ABS(YS-YT).LE.4.5) THEN
            TX=XT
            TY=YT
            NP=4
            ENDIF
          ENDIF
         ENDIF
        ELSE
        M=(YF-YS)/(XF-XS)
        ENDIF
       C=YF-(M*XF)
       CT=YT+((1/M)*XT)
       XI=(CT-C)/(M+(1/M))
       YI=M*XI+C
       DISTSQ=(XI-XT)**2+(YI-YT)**2
       DIST=SQRT(DISTSQ)
        IF(DIST.LE.4.5) THEN
        TX=XT
        TY=YT
        NP=5
        ENDIF
       RETURN
       END
C *** SUBROUTINE GUTTER
       SUBROUTINE GUTTER(XS,XF,YS,YF,GX,GY,NO,NG)
       REAL*8 XS,XF,YS,YF,GX,GY
       XG=-2000
       YG=-2000
       IF (NG.EQ.1) THEN
        AI=(YF-YS)/(XF-XS)
        D1=A1*(XG-XS)
        YN=YS+D1
         DO 10 I=0,5000,1000
           IF (YN.LE.(I+50).AND.YN.GE.(I-50)) THEN
```

```
          IF (YN.LE.(I+50).AND.YN.GE.(I-50)) THEN
          NO=6
          GY=I
          GX=XG
          ENDIF
10        CONTINUE
       ELSE IF (NG.EQ.2) THEN
        A1=(YF-YS)/(XF-XS)
        D1=(YG-YS)/A1
        XN=XS+D1
          DO 20 I=0,4000,1000
          IF (XN.LE.(I+50).AND.XN.GE.(I-50)) THEN
          NO=6
          GX=I
          GY=YG
          ENDIF
20        CONTINUE
       ENDIF
       RETURN
       END
.bottom.
```

Appendix 5

Listing of the trap data

For reasons of space it is impractical to list the complete data. Thus in the following pages the raw pitfall data from Staddon Heights is presented. This was stored in a mainframe computer file, consisting of 11 columns. The first three columns identify the date and trap, whilst the others record the numbers of each species. In 1983 and 1984 the data was stored in 23 columns, but the paucity of species at Rumleigh and Staddon Heights made this unecessary. The species stored in each column varied from site to site. Data could be rapidly sorted or summed (i.e. daily, weekly, Line totals or Row totals) using a suite of Fortran programs.

The columns at this site are listed below.

C1- Days after start of trapping

C2- Line number

C3- Row number

C4- Nebria brevicollis

C5- Trechus quadristriatus

C6- Bembidion lampros

C7- Pterostichus melanarius

C8- Calathus fuscipes

C9- Amara aenea

C10- Harpalus rufipes

C11- All other carabid species

```
 4 1 1 0 0 0  2 0 0 0 0        6 6 4 0 0 0  1 0 0 0 0
 4 1 2 0 0 0  0 0 0 0 0        6 6 5 0 1 0  0 0 0 1 0
 4 1 3 0 0 0  4 0 0 0 0        8 1 1 0 0 0  2 2 0 0 0
 4 1 4 0 0 0  4 0 0 0 0        8 1 2 0 1 0 13 2 0 1 0
 4 1 5 0 1 0  7 0 0 0 0        8 1 3 0 1 0  6 2 0 1 0
 4 2 1 0 0 0 13 0 0 0 0        8 1 4 0 0 0  2 0 0 0 0
 4 2 2 0 0 0  7 0 0 0 0        8 1 5 0 0 0  1 0 0 0 0
 4 2 3 0 3 0 16 0 0 0 0        8 2 1 0 0 0  1 0 0 0 0
 4 2 4 0 2 0  4 0 0 0 1        8 2 2 0 0 0  3 0 0 0 0
 4 2 5 0 0 0  2 0 0 0 0        8 2 3 0 0 0  2 0 0 0 0
 4 3 1 0 0 0  3 0 0 0 0        8 2 4 0 4 0  2 0 0 1 0
 4 3 2 0 1 0  3 0 0 0 0        8 2 5 0 0 0  3 0 0 0 0
 4 3 3 0 0 0 23 1 0 0 0        8 3 1 0 2 0  1 0 0 1 0
 4 3 4 0 1 0  3 0 0 0 0        8 3 2 0 0 0  1 0 0 0 1
 4 3 5 0 0 0  0 0 0 0 0        8 3 3 0 0 0  3 0 0 0 0
 4 4 1 0 0 0  1 0 0 0 0        8 3 4 0 0 0  4 0 0 0 0
 4 4 2 0 0 0  5 0 0 0 0        8 3 5 0 0 0  2 0 0 0 0
 4 4 3 0 0 0  4 1 0 0 0        8 4 1 0 0 0  2 1 0 0 1
 4 4 4 0 0 0  5 0 0 0 0        8 4 2 0 0 0  1 0 0 0 0
 4 4 5 0 2 0  3 0 0 0 0        8 4 3 0 0 0  1 0 0 0 0
 4 5 1 0 0 0  3 0 0 0 0        8 4 4 0 2 0  2 0 0 2 0
 4 5 2 0 0 0  0 0 0 0 0        8 4 5 0 0 0  2 0 0 0 0
 4 5 3 0 0 0  1 0 0 0 0        8 5 1 0 1 0  2 0 0 0 0
 4 5 4 0 0 0  1 0 0 0 0        8 5 2 0 0 0  2 0 0 0 0
 4 5 5 1 0 0  5 0 0 0 0        8 5 3 0 0 0  1 0 0 3 0
 4 6 1 0 0 0  0 1 0 0 0        8 5 4 0 0 0  2 2 0 0 0
 4 6 2 0 0 0  1 0 0 0 0        8 5 5 0 2 0  1 0 0 0 0
 4 6 3 0 0 0  0 0 0 0 0        8 6 1 0 0 0  3 0 0 0 0
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