



THE POPULATION ECOLOGY OF SOME WOODLAND CARABID BEETLES,
WITH PARTICULAR REFERENCE TO THEIR DISPERSIVE BEHAVIOUR.

by

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"We went to all the places which a beetle might be near,
And we made the sort of noises which a beetle likes to hear,
And I saw a kind of something, and I gave a sort of shout:
"A beetle-house and Alexander Beetle coming out!" "

A.A. Milne.

ABSTRACT

The Population Ecology of some woodland carabid beetles, with particular reference to their dispersive behaviour.

The mobility of carabid beetles in the field has been studied by a number of researchers in recent years, but the small scale movements are still poorly understood. The populations of five species of carabid beetles living in a Surrey oakwood were therefore investigated using pitfall trapping and individual marking techniques over a period of three years.

Five aspects of the complications associated with the interpretation of pitfall trapping and mark-release-recapture studies were investigated: (i) baiting of the traps by the catch itself, (ii) escape ability of captured beetles, (iii) changes in behaviour following overlong procedures between capture and release, (iv) density effects produced in trapping, and (v) effects of marking procedures on behaviour and survival. No effects could be demonstrated for (i), (iv) and (v). However, the escape rate in Nebria brevicollis was shown to be very high, and the behaviour of the same species affected by the length of time between capture and subsequent release.

More than 3000 recaptures of marked beetles were made. Survival into a second breeding season was found to be commonplace in all five species; a few even entered a fourth. The distributions of the beetles within the study area were aggregated, particularly so in Nebria, where it was also shown that the beetles tend to remain in the areas where they are in the highest densities. Distributions changed little with season.

Peak displacement rates were associated with the breeding season

in Nebria but, whereas this fell off with the onset of winter in first season beetles, the level remained high in second season individuals. Pterostichus madidus exhibited a significant lack of displacement with time, except with males during the breeding season. Greatest activity and dispersal was found in August in first season males, but June and July with second season. Abax parallelepipedus beetles were found to be most active early in the season. Very few beetles of the species were found to disperse 100 metres or more within the study area.

The concept of home range was examined in relation to ground beetles. Site attachment could not be demonstrated in any species, although other aspects of the trapping results indicated some form of home ranging behaviour.

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Chapter 1
Introduction

The basic aim of this study is to investigate the mobility of carabid beetles under field conditions: to study the extent of the movements of individual beetles within their habitat and during their normal daily, seasonal and annual activities, and to relate the resulting information to the life histories of the species under investigation. As recently as 1967, Chauvin remarked that the "mean area of displacement" is one of the least studied features of insects, and went on to question the usefulness of discussions on the equilibrium of insect populations lacking such basic information. This was less true of carabid beetles than for many groups.

Carabids have been the subject of much ecological research over the last twenty five years, and important early work on their local movements was conducted by Drift (1951 and 1959), Greenslade (1961), and Grüm (1962). These studies combined the use of pitfall traps to collect the beetles with mark-release-recapture and individual marking techniques. In this, methods have changed very little over the years, although recent work using radioactive labels (Baars, 1979) indicates the potential for future studies. Low density populations, high mobility, and nocturnal activity greatly interfere with quantitative investigation. Hence, information on behaviour must be obtained by indirect methods such as trapping.

A high proportion of carabid mobility research has been carried out within deciduous woodlands. The present study originated in a number of questions left unanswered by these studies. For example, it is a common practice to build up an experimental stock of beetles in the laboratory, using field sources, before releasing them at fixed points on the study site, either collectively or in groups

(e.g. Greenslade, 1961). The effects of this procedure on the subsequent behaviour and on the relevance of the results to natural populations has been little considered. There seems to be a basic assumption that individual beetles do not possess a home area, that beetles released in an "unfamiliar" area do not behave any differently to those released in an area previously explored; that male and female, immature and mature, beetles do not behave differently. Few workers, if any, have seriously tested these assumptions. Only in a few published studies are the individual beetles released at, or near to, their point of capture following marking procedure (e.g. Grüm, 1965; Mason, 1972; Haines, 1973).

Mobility throughout the full seasonal cycle has often not been investigated. Food availability, through the seasonal cycles of other invertebrates, seeds and other vegetable matter, will vary considerably, as will the suitability of environmental conditions for successful breeding. It is highly probable therefore that there will be a seasonal cycle of carabid mobility.

Haines (1973) thought it unlikely that the concept of a "home range", as used by mammalogists, is applicable to the Carabidae, with their apparently solitary hunting or scavenging habit. However, beetles have been found in apparently regularly used burrows in field situations (Cole, 1946; Frank, 1966; Mason, 1972), and usually construct similar excavations when kept in soil tanks in the laboratory (Mason, 1972; Haines, 1973). If these burrows are regularly used, then the beetles must be maintaining their foraging activities within the area around the burrow: they must be aware in some way of the immediate landscape surrounding the burrow in order to be able to find

their way back after foraging. This fits the mammalogists' description of a home range : the area used by an individual in the course of its normal activities, and implies that it is a stable area of woodland floor.

In the years before the present study was initiated, a number of observations were made in a garden of a residential London suburb (Alexander, unpubl. 1973). Various Carabidae (mostly Pterostichus madidus) encountered beneath scattered rocks were given individually-recognisable marks using a plastic-based paint. Subsequent observations indicated that many of the beetles remained beneath the same, or closely neighbouring, stones over periods of some weeks, although not necessarily being present on consecutive days during these periods. As indicated above, this result does not concur with published information on mobility in this species. The garden observations were few in number, but concerned relatively undisturbed beetles. As already mentioned, few authors have considered the disturbance effects of their experimental technique, and it was in these techniques that the answer to these conflicting results was initially sought (Chapter 3). This chapter also considers other experimental technique-based questions, and discusses the basis for the method actually used in the present study.

Following the analyses of the methods of study to be used, the life cycles of the species need to be understood before the part played by mobility can be investigated and correctly interpreted (Chapter 4). Details of the life histories of British Carabidae are generally only poorly known. However, the larger, woodland, species have been the subject of many of the previous studies referred to above, and their life histories are relatively well-known. Information on

life history, and related considerations, from the results of the present study are collated and compared with published material in order to form as sound a base as possible for the interpretation of the results of the mobility studies.

The site chosen was an area of native deciduous woodland (Chapter 2). The woodland environment is far stabler on the whole than the garden one, and so would be expected to be more conducive to home ranging behaviour. Few studies have investigated the garden Carabidae (e.g. Nield, 1974). Interestingly, the site is only a few miles from that investigated by Greenslade (1961), Silwood Park, and also occurs on the same geological formation. Life history details should be most comparable with those found in his study.

Although a few species of Temperate Region Carabidae climb within the vegetation, and/or fly in search of food, etc., the vast majority of species are restricted in foraging activity to the soil and litter layers (Kulman, 1974). Tree trunks may, however, be treated by the beetles as extensions of the woodland floor (Evans, 1975).

Following the suggestion of home ranging in Carabidae, a series of field experiments were designed in order to investigate the dispersive behaviour of the commoner, large Carabidae in the woodland study site. If individuals have home ranges, this should show up using standard mark-release-recapture techniques.

Initially the individual beetles were studied with a minimum of disturbance - physical, temporal and spatial - to give information on the nett displacement with time (Chapter 5). The results of this study would then be used in deciding the next stage of operations.

Once quantitative evidence was produced for home-ranging, the effects of experimental displacement of individuals could be investigated (Chapter 6). This would extend the information already gained on the size of the home areas by detecting changes in the beetles' behaviour. Direct observation of the movements of individuals in the fields was not seriously attempted because of the inherent difficulties in following small animals in the field at night. However, individual beetle recapture histories were examined to see how the statistically-derived conclusions appeared at the individual level (Chapter 7).

The general abundance of Carabidae in Temperate ecosystems suggests that they must play an important role in the foodwebs of their habitats. Drift (1951) has stressed the importance of the larger species, as predators of soil-pupating defoliating moth and sawfly caterpillars, in the balance of the woodland community. He later (1959) described work by Besemer (1942) on the regulation of pine sawfly (Diprion pini Linn.) populations by Carabid predation of the larvae which are exploring the soil surface in search of pupation sites. More recently, Frank (1967a,b,c) and East (1974) have continued the work of Varley and Gradwell (e.g. 1963) on the population dynamics of the wintermoth (Operophtera brumata Linn.). Frank (1967c) described an aggregative response of the carabid Pterostichus madidus to high pupal densities of this moth in the oak leaf-litter and soil. Such a response is in direct opposition to any home ranging ideas, but once again precise evidence at the individual level was not found. The aggregation suggestion followed analysis of pitfall catch size and not of movements of individually marked beetles.

If home ranging does occur in the Carabidae, then the ranges must

overlap considerably. Thus, the "aggregative response" may merely reflect increased activity of the "local" individuals which are concentrating their foraging effort on a good food source within their overlapping home foraging areas. Selection of a particular prey species when that species is present in abundance is a well-known feature of predator-prey relationships (see Chapter 8). Thus, Frank's results do not necessarily indicate nomadic behaviour, as opposed to home ranging.

In addition to forestry and agricultural pest control, the understanding of carabid mobility is also relevant to nature conservation, biogeography, palaeontology and archaeology. Although only the commoner species of carabid have been well-studied, conclusions based on these studies should help towards a sounder basis for the understanding of the distributions of our rarer species and their conservation management requirements, particularly in the acreage of nature reserves needed. The colonisation aspect, both within the species range and as extensions to that range, are of great interest in biogeography, and knowledge of a species' habits under existing conditions forms an invaluable basis for the interpretation of fossil remains in archaeology and palaeontology (see Coope, 1970, for example).

The overall aim of this study then, is to reach an understanding of the net effects of carabid locomotion on the distribution of individuals within the population; to answer the questions: (i) if an individual beetle is present at one location on one day, how far will it be from that location on successive days, (ii) will its distance from its original capture point increase with time (unidirectional dispersal), fluctuate greatly (nomadism), or remain small and

relatively constant (home-ranging). In this way it was hoped that judgements concerning drift of populations into adjoining areas of similar habitat, and hence dispersive ability, could be made.

Chapter 2
The Study Site

2.110 Location

The work described in this thesis was carried out in Great Wood, an area of oak woodland adjacent to the Zoology Department of Royal Holloway College (National Grid Reference SU 999693). Another nearby wood, Grendon Wood, was sampled for beetles marked in Great Wood over the whole of the study period. Specimens from this second wood, and from a copse within the grounds of the Zoology Department, were used in a number of experiments where individuals from outside the study area were needed, and these will be referred to in the appropriate sections.

The altitude of Great Wood is approximately 40 metres above sea level.

2.120 Environs

Great Wood is divided in two by a farm track which has substantial ditch and bank constructions on either side (see Figures 2.1, 2.2 and 2.3). Only the north-westerly half of the wood was used in the study. To the south-east, the wood is separated from another oakwood, the Dell, by a substantially banked beech avenue. The north-western side of the wood is joined by a pine plantation, and separated from it by a now much eroded ditch and bank, and an old fence line. The fourth side, to the north-east, meets a grass meadow used for grazing cattle, and is separated from the wood by a barbed-wire fence. For a short period, in the autumn of 1976, this fence was damaged in a number of places by fallen trees and cattle entered the wood regularly. Outside that period, the fence proved effective in excluding the cattle. Grendon Wood lies beyond this meadow.

Figure 2.1 Great Wood and its environs

(traced from aerial photograph held in Zoology Dept., R.H.C.)

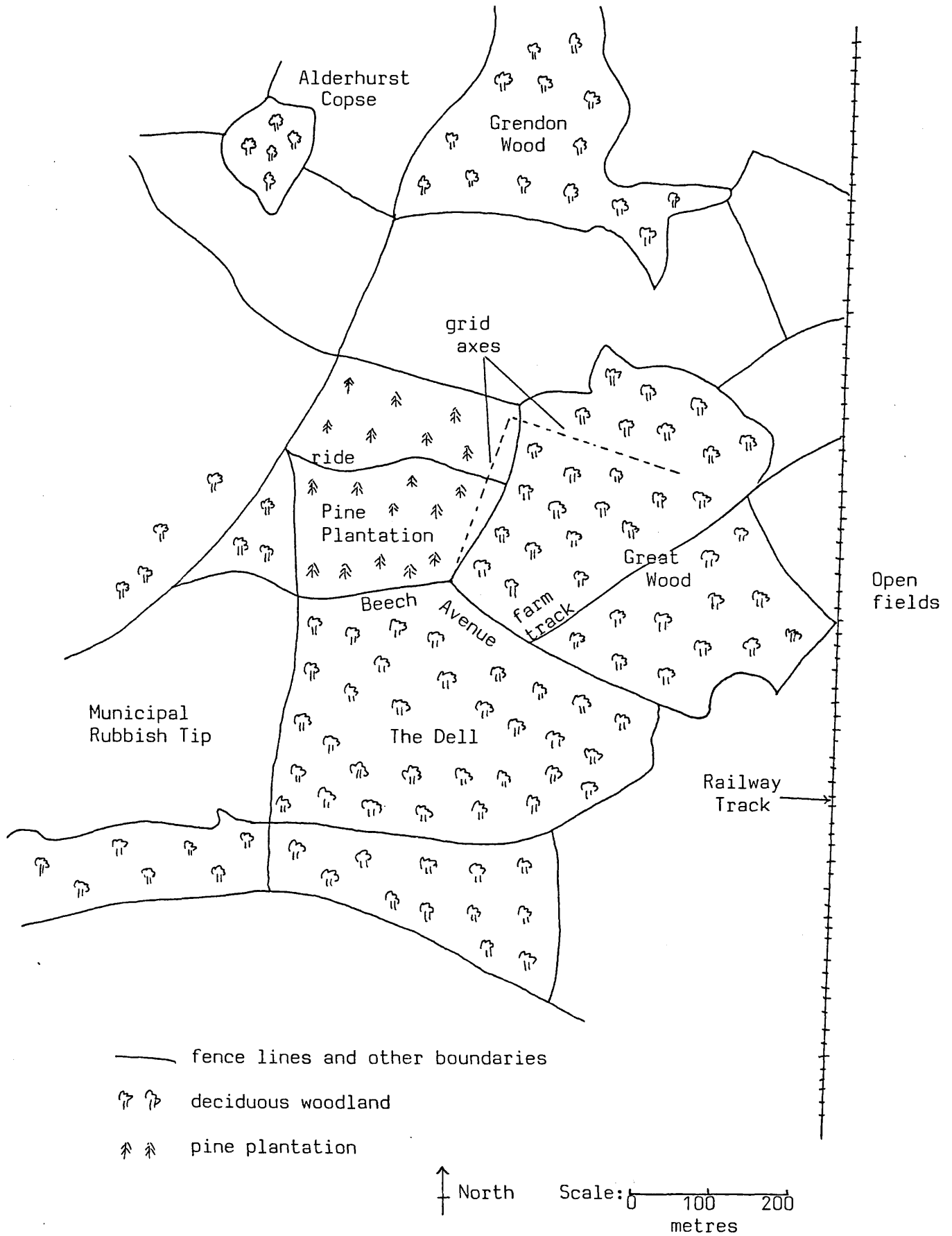
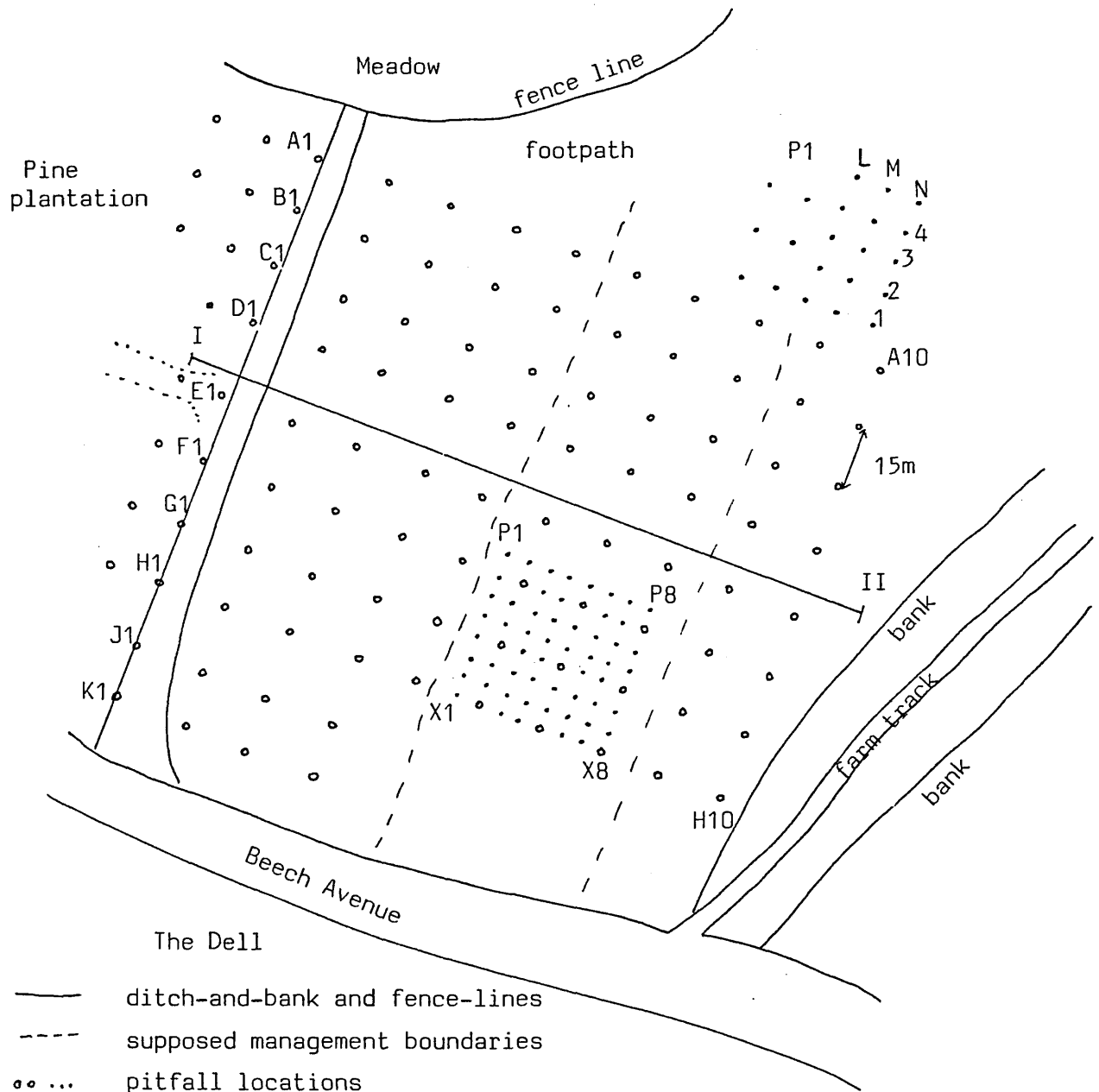


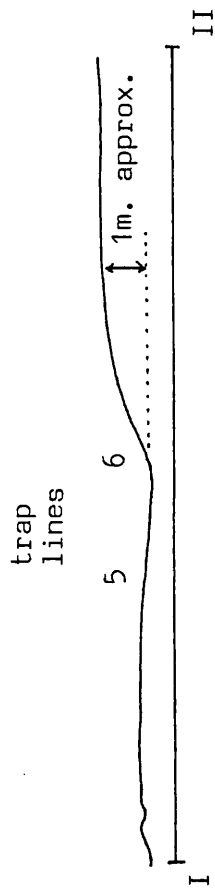
Figure 2.2 Layout of pitfall grids in Great Wood



- ditch-and-bank and fence-lines
- - - supposed management boundaries
- pitfall locations
- A1, K1 pitfall locality code numbers
- I—II line of cross section (Fig. 2.3)

[the grids A1-A10-G1-G10 and P1-P8-X1-X8 are the main ones used in the following investigation. A1-A10-G1-G10 was replaced by A1-A10-H1-H10 during the second year of studies.]

Figure 2.3 Section across centre of trap grid to show central low-lying area of Great Wood



2.200 Geology

Great Wood stands on a layer of Bagshot Sands, less than one metre thick, overlying London Clay. The sands in this area contain seams of pebbles, some of which are brought to the surface by the activities of mammals such as rabbit, fox, badger and man.

The high ground on which the wood stands falls away to the east where Thames flood plain gravels predominate. The underlying clay layer prevents rapid drainage of water in the wood, and the soil remains moist for much of the year.

2.300 Vegetation

The dominant species of tree in Great Wood is the pedunculate oak (Quercus robur L.) and the flora conforms well with that described by Tansley (1952) as associated with a "dry oakwood". A dense growth of bramble (Rubus fruticosus Abb.) is found in the central low-lying area, towards the south-western corner, and in a smaller area in the south-eastern corner. Elsewhere bracken (Pteridium aquilinum L.) predominates, but only forms a dense closed canopy in the few areas where the oak canopy is thinner. The deep shading of oak and bracken excludes grasses from all but a very few locations (Fig. 2.4). In the spring a strong growth of bluebell (Endymion non-scriptus L.) is characteristic of the wood edge bordering the plantation of Scots pine (Pinus sylvestris L.). Towards the eastern side of the wood the dominant plant is bilberry (Vaccinium myrtillus L.), forming a very dense tangle throughout this part of the wood, and separated from the rest by what appears to be a boundary of past management. This will be referred to again later (2.400).

In the central, low-lying, area (see Figure 2.3), oak is replaced

Figure 2.4 Vegetation Maps of Great Wooda) Canopy-forming species:-

	A	B	C	D	E	F	G	H
10	O	B	B	O	O	S	O	O
9	O	B	O	B	O	O	O	O
8	O	O	O	O	-	O	O	O
7	O	O	O	O	O	O	O	O
6	O	O	O	O	O	O	O	O
5	O	O	O	B	B	B	O	O
4	O	P	O	O	O	B	O	O
3	B	P	B	O	O	O	O	O
2	S	B	P	-	O	O	S	B
1	P	P	P	P	O	P	P	P
	P	P	P	P	P	P	P	P

O oak
- nil
S rowan
B birch
P pine

b) Shrub-layer:-

B	vb	Vb	vb	V	V	b	b
b	V	vb	vb	vb	V	B	b
hb	b	b	B	B	b	b	b
b	b	b	b	b	b	r	r
rh	rhb	b	hb	H	hb	hb	hb
b	RD	R	Rb	Rb	R	hb	hb
hb	b	rb	hb	b	bG	r	r
b	B	b	hb	R	R	R	R
Rb	Rb	b	B	r	r	R	R
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-

V bilberry
R bramble
H holly
B bracken
D male fern
G grass
[small letters
denote sparse
vegetation]

by birch (Betula pendula Roth), and, also in this area, holly (Ilex aquifolium L.) bushes are present at their greatest density, spreading out into the adjacent oak areas. This area seems to be where water drains off the surrounding woodland since the ground here is usually wet and often floods during heavy rainfall. Drainage is to the north-north-east.

The overgrown ride between Great Wood and the pine plantation has, in contrast with the oakwood, a great diversity of trees and shrubs : sycamore (Acer pseudoplatanus L.), hazel (Corylus avellana L.), beech (Fagus sylvatica L.), sweet chestnut (Castanea sativa Miller), hawthorn (Crataegus monogyna Jacq.), alder (Alnus glutinosa L.), elder (Sambucus nigra L.) and rowan (Sorbus aucuparia L.). Other plants with localised but vigorous growth in the oakwood include broad-buckler fern (Dryopteris dilatata Hoffm.), honeysuckle (Lonicera periclymenum L.) and common fumitory (Fumaria officinalis L.).

The pine plantation, having been planted with a high density of trees, has little plant growth as understorey. Sycamore seedlings are commonest here but generally die within a few years, except where there is a break in the canopy due to tree mortality, or in the single ride running directly away from the centre of its edge with Great Wood.

Great Wood is separated from the Dell by an avenue of ancient beech trees.

The almost complete canopy of oak suppresses the vigour of the ground vegetation, and bare litter predominates over much of the wood.

Plant nomenclature follows Clapham, Tutin and Warburg (1968).

2.400 History of the Site

"A wood's pedigree is the key to its ecology" (Tubbs, 1977), Great Wood consists of old coppiced oak : coppicing prolongs the life of the tree so the stools may be several hundred years old. It is a form of management that requires little or no replanting and the woodland is likely to retain ecological links with earlier times. The boundaries of the wood show the characteristic ditch and bank of medieval woodland in many places.

For centuries most of the woods of southern England were managed as "coppice-with-standards" in which the underwood was cut on a relatively short rotation to supply essential commodities such as firewood and hurdling material, while the standards were allowed to grow on to be cropped selectively for building timber (Tubbs, 1977). Oak coppices freely when cut up to at least 150 years growth (Rackham, 1974). The root system is not damaged and many new shoots arise from the stools, some of which become dominant and establish a complete canopy in as short a time as 4 - 10 years (Ash and Barkham, 1976).

An old stool spreads, without loss of vigour, into a ring of living tissue with a decayed centre and often an interrupted circumference (Rackham, 1976). Eventually the stools may become badly rotted and, as the shoots get larger, there is considerable risk of damage by wind throw. As a result old, dead and dying trees are numerous in such woodlands. Great Wood is currently at this stage.

Rackham (1974) remarks that, since 1945, most of the remaining woods have retained their historical continuity but are no longer managed. The most recent coppicing in Great Wood appears to have been no less than 25 or 30 years ago, and so fits in well with Rackham's picture.

A distinct rotational pattern of coppicing is noticeable in Great Wood. Those trees with the smallest regrowth shoot are in the eastern section, and are separated from the medium age-group by a break (see Figure 2.2) - there is no visible evidence for this having been a ride. The largest regrowth trees lie between the low-lying area and the pine plantation and, incidentally, is the only area with oak standards.

Great Wood was linked with Grendon Wood up until some time between 1860 and 1940, when the ground between today's woods was cleared for use as grazing land for cattle. The link was on the gravels around the base of the sands on which the present day remnants of the larger wood stand.

Further evidence for the age of this wood is found in the presence of two species of dead-wood inhabiting beetle considered to be characteristic of primary woodland in Britain (Harding, 1978): Stenagostus villosus (Elateridae) and Rhizophagus nitidulus (Rhizophagidae).

The pine plantation is of recent origin and consists of even-aged trees of no more than 30 year's growth.

2.500 Weather 1975 - 1978

The exceptional weather conditions experienced during part of this study merit special note. The period May 1975 until August 1976 was the driest 16 months in England and Wales since records began in 1727 (Murray, 1977). September was the only month that was generally wet. In addition, temperatures were higher than average - the winter of 1975 - 76 combined extreme dryness with above normal temperatures (Perry, 1976), and the summer was the hottest for 150 years (Meaden, 1976). This especially severe drought ended abruptly with the highest

September and October rainfall on record (Ratcliffe, 1977).

The combination of heat and drought which persisted through the summer months of 1976 would appear to be unparalleled in modern times. Therefore, the results of field studies conducted over this period require careful interpretation. Some features of the trapping figures for 1976 are distinctly different from the following two activity seasons, and may well be a direct consequence of the extreme conditions (see 4.600 for example). It should be noted, however, that the springs which occur in the study site did not completely dry out, and so will have buffered the more extreme effects.

Maximum and minimum temperatures were recorded in the wood throughout the study period, and the monthly figures are given in the appendix.

2.600 Carabidae found in Great Wood, 1975 - 78

	Total catch of adults in pitfalls	Other sources of adults in greater numbers
<u>Cychrus caraboides</u> (Linnaeus)	17	
<u>Carabus nemoralis</u> Müller, O.F.	1	
<u>C. violaceus</u> Linnaeus	167	
<u>Leistus ferrugineus</u> (Linnaeus)	14	
<u>L. fulvibarbis</u> Dejean	21	
<u>L. rufomarginatus</u> (Duftschmid)	126	
<u>L. spinibarbis</u> (Fabricius)	22	
<u>Nebria brevicollis</u> (Fabricius)	6463	
<u>Notiophilus biguttatus</u> (Fabricius)	593	
<u>N. rufipes</u> Curtis	677	
<u>N. substriatus</u> Waterhouse, G.R.	4	
<u>Loricera pilicornis</u> (Fabricius)	10	
<u>Asaphidion flavipes</u> (Linnaeus)	3	day-active on bare ground
<u>Bembidion lampros</u> (Herbst)	12	
<u>B. tetracolum</u> Say	4	

	Total catch of adults in pitfalls	Other sources of adults in greater numbers
<u>B. guttula</u> (Fabricius)	8	
<u>B. unicolor</u> Chaudoir	3	
<u>Stomis pumicatus</u> (Panzer)	65	
<u>Pterostichus angustatus</u> (Duftschmid)	1	
<u>P. diligens</u> (Sturm)	2	
<u>P. madidus</u> (Fabricius)	4770	
<u>P. niger</u> (Schaller)	433	
<u>P. nigrita</u> (Paykull)	20	
<u>P. strenuus</u> (Panzer)	2	
<u>Abax parallelepipedus</u> (Piller & Mitterpacher)	1369	
<u>Calathus fuscipes</u> (Goeze)	493	
<u>C. melanocephalus</u> (Linnaeus)	2	in rotten wood during winter
<u>C. piceus</u> (Marsham)	525	
<u>Laemostenus terricola</u> (Herbst)	13	
<u>Agonum assimile</u> (Paykull)	11	
<u>A. marginatum</u> (Linnaeus)	1	
<u>A. muelleri</u> (Herbst)	20	
<u>Amara aenea</u> (Degeer)	29	
<u>A. communis</u> (Panzer)	1	
<u>A. convexior</u> Stephens	1	
<u>A. familiaris</u> (Duftschmid)	1	
<u>A. plebeja</u> (Gyllenhal)	7	
<u>Harpalus rufipes</u> (Degeer)	4	
<u>H. affinis</u> (Schrank)	1	
<u>H. rubripes</u> (Duftschmid)	1	
<u>H. tardus</u> (Panzer)	1	
<u>Anisodactylus binotatus</u> (Fabricius)	1	
<u>Bradycellus sharp</u> Joy	15	
<u>Acupalpus meridianus</u> (Linnaeus)	1	
<u>Badister bipustulatus</u> (Fabricius)	2	
<u>Dromius agilis</u> (Fabricius)	-	on and under bark
<u>D. quadrimaculatus</u> (Linnaeus)	-	" " " "
<u>D. quadrinotatus</u> (Zenker)	-	" " " "
<u>Metabletus foveatus</u> (Fourcroy)	63	
49 species	Total adults	
		16,000

Total trap days 65,826 i.e. on average 1 adult taken every 4.1 trap day.

Nomenclature and order follow Kloet and Hincks (1977). Adult carabids were identified using Lindroth (1974) and Joy (1932), and larvae using van Emden (1942), Davies (1963), and Luff (1969, 1972, 1976), by comparison with specimens loaned by Dr. M.L. Luff, and by rearing to adult. The sexes of the adults were separated using Lindroth (1974) and Kevan (1949). The sexes of Nebria brevicollis were not separated during the first year of the study due to difficulties experienced in identification.

Chapter 3
Methods

3.100 Introduction

This study is concerned with the movements of individually recognisable beetles under field conditions. The sampling methods must be designed to demonstrate these movements and provide sufficient individuals for the conclusions reached to be statistically sound.

The techniques involved can conveniently be classified to three levels : capturing, marking, and releasing. It is important that neither the beetles nor their habitat are unduly disturbed by the study - the effects of the experimenter must be kept to a minimum.

3.200 Capture Techniques

3.210 Introduction

The first stage of any study of animals in the field is location of the individuals. The nocturnal woodland ground beetles can be found by a number of methods:- (i) direct observation, (ii) soil and litter sampling, (iii) examination of daytime refuges, and (iv) pitfall trapping. These will now be considered individually as an introduction to the methods actually used in this study.

3.220 Direct Observation

An accurate picture of the beetles' movements during their active periods may be gained by following individuals in the field. However, this approach has a number of difficulties which cannot all be completely overcome at present. The first is the recognition of the individual beetles. The observer must be sure that he is following the same individual throughout the observation period. The nature of the litter habitat makes this impossible unless the beetle has, or is given,

individual characteristics recognisable to the observer at a distance. The beetles are unlikely to be in view continuously and so reappearances need to be confirmed as the same individual. Marking techniques will be considered later (Ch. 3.500), but it is sufficient to say here that the application of marks involves disturbance of the beetles. Therefore, their behaviour on release cannot be considered typical. The beetles must be given time to recover from the disturbance. Here another problem arises. The chances of relocating the marked individuals under field conditions are relatively small even when using fluorescent or radioactive labels. To overcome this problem, large numbers of beetles need to be marked and released. The marks could be of a fluorescent dye so that they will be relatively invisible to predators, and yet readily visible to the experimenter using a UV lamp.

A major criticism of the technique is that, at any one moment, only one individual can be observed. Simultaneous observations of a number of individuals are essential if valid conclusions about the population as a whole are to be made. Also, no information is produced on the density or distribution of the beetles within the study site. The length of observation period is difficult to standardize as it depends, amongst other things, on the beetle itself, and yet standardisation of observations is essential for valid comparisons of individuals.

Another important point is that if the observer remains close enough to the beetle to follow its movements precisely, then the beetle may become aware of the observer and react accordingly. In either case the observer is altering the structure of the soil surface and vegetation over large areas of the wood by tread.

The most attractive method used to date is the tracking of radio-

actively labelled individuals. Baars (1979) has successfully studied the short-term dispersive behaviour of some heathland beetles by combining a radio-active label with individual marking, and his results have great bearing on the interpretation of those from the present study. However, most of his beetles died from the effects of the radiation within seven weeks.

3.230 Soil and Litter sampling

The extraction of beetles from soil and litter samples has been used to gain accurate figures for population density (Briggs, 1961; Greenslade, 1964c; Evans, 1969). However, ground beetle populations exist at very low densities in woodland (Tipton, 1960; Greenslade, 1964d; Grüm, 1971; Haines, 1973), and so large volumes of litter and soil need to be examined before sufficiently large numbers are taken to estimate density accurately. The technique is obviously of very limited use in studies of movements of individual beetles since large areas of the soil surface need to be disturbed, and it is impossible to differentiate between members of the active population resting between bouts of activity, and individuals still quiescent after hibernation, or aestivation, or before emergence after pupation (Greenslade, 1964d).

In addition, some authors have found that some ground beetles make, and apparently regularly use, burrows in the soil (Cole, 1946; Frank, 1966; Mason, 1972). These would be destroyed by this sampling technique, and the normal behaviour of the beetles in using burrows changed.

However, the technique is useful as a check on population estimates derived from mark-release-recapture studies, and as a straight comparison with pitfall catches.

3.240 Refuges

The nocturnal ground beetles shelter from the light during the daytime. The refuges chosen vary from burrows (Cole, 1946; Frank, 1966; Mason, 1972) and cracks (Kirk, 1973) in the soil surface, to hiding beneath leaf litter, logs and stones. In Great Wood, large surface refuges, such as logs and stones, are uncommon and the beetles are more frequently found beneath the litter and in the soil.

An alternative to sampling natural refuges is to introduce artificial ones, or "cryptozoa boards" (Cole, 1946). Boards or tiles are placed on the ground in the hope that they will be used as refuges. This method has been used by a number of authors (Cole, 1946; Gilbert, 1956; Briggs, 1961; Greenslade, 1961; Giles, 1970), but with varying results.

The advantages of this approach are: (i) the beetles themselves choose to remain under the boards, (ii) the beetles are readily accessible to the experimenter in the daytime, (iii) information is gained on the permanence and frequency of use of the refuges by individuals, and (iv) simultaneous sampling is possible, since the individuals are inactive throughout the daylight hours. The disadvantages are that: (i) the conditions beneath the boards are disrupted each time the experimenter displaces it - although this may be overcome with individually marked beetles by placing a transparent board/tile beneath the cover, (ii) relatively small numbers of individuals are observed, and most importantly (iii) no evidence of individual activity away from the refuge is demonstrated. Cole (1946) used control boards to test for disturbance effects. These were left undisturbed for periods of up to one year, but showed no significant differences in inhabitants

from the experimental boards.

During the present study, two boards were placed within the study site and examined regularly for one year, in which time only a single Abax parallelepipedus was found, and only on one occasion. The boards proved more attractive to Myrmica ruginodis ants which rapidly colonised them. Gilbert (1956) also experienced this problem. Thiele (1977) mentions information derived from Lindroth to the effect that ground beetles and other litter inhabitants are disturbed and put to flight by the large numbers of ants present in the colonies.

3.250 Pitfall Trapping

The commonest method of collecting surface active animals is the use of pitfall traps. With smaller animals, these consist of containers buried in the ground with the opening flush with the soil surface. Animals running across the soil surface fall over the edge and into the trap. Capture is a more complex affair than this, but this will be discussed in more detail later (Ch. 3.300).

A wide spectrum of animals has been studied in this way: small mammals (Mosby, 1960; Giles, 1970), small lizards (Turner and Gist, 1965), isopods (Hamner et al, 1969; Hayes, 1970), millipedes (Banerjee, 1970; Blower, 1970), scorpions (Hadley and Williams, 1968), spiders (Hallander, 1967; Huhta, 1971; Uetz and Unzicker, 1976), ants (van der Aart and de Wit, 1971; Greenslade, 1973), tenebrionid beetles (Turner, 1962; Rickard and Haverfield, 1965; Calkins and Kirk, 1973), and carabid beetles. Most, if not all, of the factors affecting catch size are relevant to all studies, no matter which species involved. Critical studies of the efficiency of pitfall trapping have been

conducted by Briggs (1961), Mitchell (1963b), and Greenslade (1964c), and European studies have recently been reviewed by Thiele (1977).

The main advantages of pitfalls are:- (i) large numbers of individuals are collected, (ii) samples can be taken from many areas simultaneously, (iii) the traps can be operated daily for very long periods with minimal attention from the experimenter, (iv) habitat disturbance is minimal, and (v) the intensity of sampling is standardised for all locations. These are counteracted by the disadvantages: (i) activity and abundance are inseparable (Briggs, 1961; Greenslade, 1964; Southwood, 1966) and (ii) the beetles' activity is interrupted for part of the night at least, and they lose the choice of daytime refuge. Other characteristics of the technique will be discussed later (3.300).

A modification of the basic pitfall is the introduction of a time-sorting mechanism (Williams, 1958; Holm and Edney, 1973; Barndt, 1976) whereby a series of collecting tubes individually receive the catch at different times of the day.

The basic pitfall has also been elongated as a "gutter-trap" (Fairhurst, 1969; Haines, 1973; Nield, 1974; Luff, 1975b). Here, halved hollow cylinders are placed in the ground with standard pitfalls at either end. Animals falling into the gutter accumulate by their own activities in the end pitfalls. These have the advantage of confronting the mobile animals with a long perimeter in their path, thus increasing the chances of interception. Such traps have been used mainly in enclosing areas completely in order to study movement into, and out of, fixed areas of habitat. Their main disadvantage is in the loss of information on the precise point of capture of individuals, and so

are of little value if evidence of home ranging behaviour is sought. Such traps are also more prone to flooding and choking with leaves, branches, and so on, because of the greater area open to the air, and also to external predation for the same reason, as well as being more obvious to small mammals and birds.

When not in use, the simple pitfall may be closed merely by inverting it inside the pit. More elaborate pitfalls may require more elaborate closing mechanisms.

3.260 Conclusions

It is evident from the preceding sections that pitfall trapping is the method most suited to the needs of this study. Direct observation is fraught with difficulties, the most important being the absence of controlled information production. Much time is used up in producing information on only single individuals. Refuges disturb the animals and the site least, but do not produce evidence of activity or information on the extent of that activity. Soil and litter sampling involve too much habitat disturbance.

Pitfall-trapping has come under heavy criticism in the past (Briggs, 1960; Greenslade, 1964; Southwood, 1966; Hayes, 1970; Thomas and Sleeper, 1977), but it remains the most efficient means of obtaining ground beetles, and, combined with an individual marking technique, some of the disadvantages may be avoided. Pitfall trapping allows simultaneous sampling at a large number of locations, and demonstrates activity, and is, therefore, superior to all other methods as far as the needs of this study go. It is essential, however, that all sources of irrelevant variation in catch size be known, and, if possible, eliminated.

3.300 The pitfall trap : sources of variation in catch size and composition

3.310 Introduction

It has already been mentioned that the catch in a pitfall trap and the total catch of a grid of traps are the result of many complex interactions (Ch. 3.250). Many authors have discussed these and some have gone on to investigate certain features experimentally. These are summarised below and relevant publications noted.

3.320 Intrinsic properties of the trap

- (i) **Material and colour:** pitfall traps should be cryptic; and the interior walls should provide minimal purchase for beetle claws, preventing escapes. (Greenslade, 1964; Fairhurst, 1969; Nield, 1974; Luff, 1975).
- (ii) **Size and shape:** the capture efficiency of the trap is directly related to the circumference of the opening. "Trapping effort" can be standardised at each trap point by use of identical containers. (Turner, 1962; Nield, 1974; Luff, 1975; Thomas and Sleeper, 1977 ; Adis, 1979).
- (iii) **use of trap accessories to overcome various problems and to increase the catch size:** a variety of trap features have been used by past authors, but these will not be detailed here. The functioning of any accessory needs to be investigated thoroughly, in case it causes additional complications. In the present study, the neutrality of the trap is all important. Therefore the use of baits, funnels, shelters, etc., was avoided.
- (iv) **Continuous usage of containers without cleaning, or regular emptying:** there is a possibility of attraction to traps due to attractive chemicals produced by other animals of the same

species, or of prey species, and similarly of a repellent effect from defensive chemicals, or emission of waste products. Evidence comes in the form of non-random distribution of beetles through the grid of traps (Frank, 1967; Ahearn, 1971; Mason, 1972) and unequal numbers of the sexes in the catch (Haverfield, 1965; Ahearn, 1971; Mason, 1972; Thomas and Sleeper, 1977). This has not been studied in the past, and is investigated in the present study (see Ch. 3.420).

- (v) Traps acting as refuges: pitfall traps are dark cavities in the woodland floor, and so may attract species which are seeking hiding places. This problem has been mentioned with regard to millipedes (Barlow, 1957) but appears to have been ignored elsewhere. The many slugs found in traps during the present study obviously fall into this category. Trap colour and surface shine are relevant.
- (vi) Capture efficiency: not all animals encountering a trap will fall into it. This will vary with species and sex. Faster moving individuals are more readily captured; slower ones may detect in time to avoid capture (Mason, 1972).
- (vii) Retaining efficiency: once captured, an animal may still be able to escape before the catch is collected, especially if the opening has been fouled by debris or the inner surfaces made less slippery by wind and dust deposition. Again, this will vary with species and sex. (Mitchell, 1959; Frank, 1967; Petruska, 1969; Luff, 1975; Thiele, 1977). This problem is investigated in Chapter 3.430.

3.330 Pitfalling Technique

- (i) Arrangement of traps: the pattern of a grid of traps is dictated

to some extent by the nature of the topography and the availability of uniform habitat. Trap "interference" - the interception by one trap of animals which might have been captured at another - is standardized by regular spacing; the edge effect is also important. A regular pattern facilitates mathematical analysis of capture results. (Mason, 1972; Thomas and Sleeper, 1977).

- (ii) Trap density: higher trap densities increase trap interference and disturbance of the study site. (Greenslade, 1961; Fairhurst, 1969; Blower, 1970; Ahearn, 1971).
- (iii) Trap numbers: Obrtel (1971) found that the use of 10 to 12 traps was sufficient "to reveal the presence of the dominant species of Coleoptera, to provide reliable data on the natural ratio among the major species, and to examine the activity-abundance of the major species of soil surface Coleoptera".
- (iv) Trapping time intervals: traps remove individuals from the active population and hence reduce the density of active animals. The confined animals may behave differently on release to those not captured. (Vlijm, et al, 1961; Falk, 1974). This is investigated in Ch. 3.440.
- (v) Removal of adjacent vegetation: changes in the habitat immediately surrounding the trap may result in changes in the catch size and composition. Species exhibit different reactions to different habitat structure. (Greenslade, 1964; Novak, 1969; Huhta, 1971).
- (vi) Digging-in effects: soil disturbance may affect behaviour of animals in the soil, and hence their predators. (Joosse and Kapteijn, 1968; Greenslade, 1973).
- (vii) Effects of visits by experimenter: compaction of soil and litter layers, and damage to the vegetation from tread. (Greenslade, 1961; Falk, 1974).

3.340 Climatic and biotic factors

- (i) Weather: catch size and composition has been shown to vary with various aspects of the local weather, e.g. humidity and temperature; rainfall may erode the soil around the trap mouth, and drought may crack the soil and cause contraction away from the trap mouth. (Drift, 1951; Tipton, 1960; Briggs, 1960; Greenslade, 1961; Mitchell, 1963; Fairhurst, 1969; Nelson, 1970; Mason, 1972; Jones, 1976; Holliday and Hagley, 1978 ; Adis, 1979).
- (ii) Surface illumination: activity varies in duration and position in the daily cycle according to species, and, to some extent, sex. This may change with season, and there is the possibility of effects due to cloud cover and lunar phases. (Greenslade, 1963; Breymeyer, 1966; Williams, 1968; Thiele and Weber, 1968; Ahearn, 1971; Barndt, 1976).
- (iii) Individual differences in behaviour: the activity of individuals and their reactions to stimuli will vary according to the "condition" of the individuals - species, sex, season, hunger, age, local population density, etc. (Drift, 1951; Gilbert, 1955; Skuhavy, 1957; Mitchell, 1959; Dempster et al 1959; Briggs, 1961 and 1965; Vlijm, 1961; Williams, 1962; Greenslade, 1964; Grum, 1971; Mason, 1972; Luff, 1973; Szyszko, 1974 and 1976; Nield, 1974; van Heerdt et al, 1976; Evans, 1977; Ericson, 1977; Ernsting, 1977).
- (iv) Changes in abundance of population: adult numbers are at their highest towards the end of the pupal eclosion period; from then onwards numbers drop steadily through death and emigration, and are only supplemented by immigration, until the next eclosion period.
- (v) Type and density of the ground vegetation: ground cover characteristics

affect species composition, and individual activity through resistance to movement. Seasonal changes in ground flora important (Heydehann, 1956; Rivard, 1965; Frank, 1967; Speight and Lawton, 1976 ; Adis, 1979).

- (vi) Nature of the soil: compactness and particle size of soil affects surface movement and any burrowing behaviour. Different species may have different substrate and chemical preferences (Krogerus, 1932; Larsson, 1939; Lindroth, 1949; Palmieri and Planonoff, 1943; Drift, 1962; Lesniak, 1972).
- (vii) Reaction of the beetles to trapping: effect of capture and subsequent release on behaviour of individuals. There may be a period of disturbance activity or inactivity. Timing of the release may be important due to the activity periodism. There is a possibility of subsequent trap avoidance or attraction; stress effects from confinement with other individuals; contact effects of mating and parasite transfer while held in the traps. (Drift, 1951; Greenslade, 1964). See also Ch. 3.450.
- (viii) Patchiness of the resources of the habitat will lead to patchiness in the distribution of the beetles (Rougharden, 1977).

3.350 Other considerations

3.351 Stochastic effects

The probability of a foraging beetle encountering a trap is important. It is highly probable that a trap in an area of high beetle density, or activity, will produce large catches, but small catches will also occur albeit infrequently. Frank (1967b) found that, although catch varied widely on a daily basis, when the total numbers caught during the whole of the trapping period for each trap of a group were compared, they differed by less than one standard deviation.

3.352 Activity and Abundance

A pitfall trap is a static trap. It is the activity of the animals which results in their capture, but it is the abundance of the active animals which determines the catch size. The inability of pitfall trapping techniques alone to separate the effects of activity and abundance has been the source of much discussion (Heydemann, 1953; Tretzel, 1955; Briggs, 1961; Greenslade, 1964; Breymeyer, 1966; Huhta, 1971). The terms "activity abundance" (Tretzel, 1955) and "density of activity" (Heydemann, 1953) have been used to describe the pitfall catch. Mason (1972) considered that pitfall catch size may be valuable as an estimate of predator pressure on the area - an idea similar to the "index of penetration" of Grum (1959).

Individual beetles are not continuously active within their activity period. Bouts of activity separated by resting periods have been described in Pterostichus madidus (Williams, 1959) and Carabus purpurascens (Kirchner, 1964). At any one moment in the main activity period there will be a spectrum of activity levels, from completely inactive to highly active individuals. The inactive individuals may be only resting between bouts of activity, or may be completely inactive throughout the trapping period. It is the actual sizes of each of the activity levels that sum to produce the "activity abundance" or "density of activity".

Changes in abundance of the populations are easy to visualise since they depend on the appearance of new generations annually, an event followed by mortality and migration. Thus changes in abundance are generally regular and slow processes. On a day to day basis little change in population density will occur. However, activity is much

more complex, being affected by a large number of factors (see Ch. 3.340), and is highly variable. Short term variation in catch size is therefore mainly the result of changes in activity.

3.353 The sampling area of the pitfall trap

As will be shown later (Ch. 5), the distances travelled in one night by a single individual can be surprisingly large. It might be considered that the area sampled is approximated by a circle, with the trap at the centre, and a radius the largest distance a beetle is found to travel in one night. The frequency distribution of the distances achieved by marked individuals in one night could then be described. In practice however, too few individuals are recaptured on the night following release for statistically valid distributions to be calculated (see Ch. 5). Since it is also known that activity levels can vary widely from night to night (see Ch. 3.340), the effective sampling area will also vary from night to night.

Even the question of the area of the entire grid plot is rather difficult. It is generally arbitrarily considered to be that enclosed by the boundary formed by the outer traps (Richard and Haverfield, 1965; Nelson, 1970; Thomas and Sleeper, 1971). However, since traps on the margin also take individuals from outside the grid, other authors add a boundary thickness equal to half the intertrap distance (Dub, 1971; Ericson, 1977). The sampling areas of adjacent pitfalls are likely to overlap to some extent creating an interference effect.

3.360 Pitfall trapping methods used in this study

The standard pitfall-trapping procedure followed throughout the study (the "control" in the following investigations into the effects of certain methods used) is as follows: All pitfall traps used were

standard-sized glass jam jars with a mouth diameter of approximately 53mm and depth approximately 100mm. All captured beetles were taken to the laboratory for examination, given individually recognisable marks (see later) if none already present, and released at a point 1m from the point of capture, all within the daylight hours following the night of capture. Thus no complete cycle of activity in the wood was missed by the beetles either through being held in the field pitfall traps or in the laboratory.

The pitfall traps were arranged in grids in the study site (see Ch. 2) in a regular chessboard pattern. Distances between traps were 15m throughout the investigations described in Chapters 5 and 6, and 5m in Chapter 7.

3.400 Investigations of certain aspects of pitfall trapping and the interpretation of catch composition

3.410 Introduction

Many of the factors which affect size and species composition of pitfall catches, and hence complicate their interpretation, have been insufficiently investigated in the past, and in some cases not at all. Therefore, it was decided that, in order to correctly analyse the results of the pitfall trapping studies described in this thesis, some further investigations were necessary. Since the main study required as long a period of operation as possible to achieve the necessary results, investigations into the characteristics of the techniques had to be undertaken concurrently. Should any feature of the techniques be found to significantly affect the results this would be corrected for at the analysis stage.

As the reactions of individuals to some stimuli may change with season, the experiments were conducted more than once a year wherever

possible.

3.420 The possibility of active aggregation of beetles in pitfall traps

3.421 Introduction

Nield (1974) remarked that "once a beetle is in a trap, it is then baited". The main lines of evidence for this idea are the observations that: (i) individual traps often catch larger numbers of beetles that would be expected from the total catch for the grid, and (ii) in these large catches one sex may predominate. The presence of powerful odoriferous glands in both sexes of carabids has been suggested as the agent of attraction.

In order to clarify the situation, a field experiment was carried out in which beetles were used as baits. If traps became effectively baited once a catch was made, then baiting from the very start of the experiment should amplify the effect.

3.422 Methods

Pitfall traps were placed in grid trap lines L, M, N and H, J, K (see figure 2.2). Three types of trap were used:- (i) clean, unused, jam jars, (ii) clean, unused, jam-jars each containing an individually marked live ground beetle as bait, and (iii) jam-jars which had been in use in the field for a period not less than one month, and so possibly carrying an odour of some description (derived from the previous catches, or the habitat itself). The large numbers of pitfall traps in operation during the study period meant that regular cleaning of the field traps, or replacement with unused traps, was not feasible. Therefore, it was felt necessary to use two controls: one a clean pitfall, and the other one which had been well-used under field conditions.

The locations of each individual trap were changed at each examination so that each location would experience each type of trap. In this way locational effects could be minimised.

The experiment was run in the breeding season (see Ch. 4) when all trapped individuals were noticeably strong smelling, and presumably at a time when attraction effects, if any exist, are at a maximum.

From 26th July until 6th August, 1978 Pterostichus madidus baits were used in 20 pitfall traps at grid locations P4 to S8 inclusive. The bait consisted of two individuals in each case and were obtained by pitfall trapping in Grendon Wood. Three different baits were used: (i) two females, (ii) two males, and (iii) one of each sex. The traps were set up in the afternoon and examined the following morning throughout the experimental period.

Similar experiments using Nebria brevicollis baits were abandoned following high loss rates of the marked bait beetles either through escaping or predation (see also 3.433). The occasional recapture of these individuals in other traps indicates the former.

3.423 Results and Discussion

The catch results (Table 3.1) were treated as a 2 x 5 Contingency Table in order to test the homogeneity of the sex ratios: $\chi^2 = 2.89$ ($0.70 > P > 0.50$), therefore no significance at the 5% level. The catch totals were also examined but again no significant difference could be found between the experimental conditions ($0.20 > p > 0.10$). Visual examination of the figures suggested that more males were captured if females were present in the traps. This was tested, but again no significant difference could be demonstrated: presence v.

absence of females in the traps produced a χ^2 of 1.68 ($0.20 > P > 0.10$) and, the same test for males, a χ^2 of 1.13 ($0.30 > P > 0.20$)

The two alternative explanations for aggregated distributions of beetles in pitfall traps are (i) location, and (ii) attraction. In the former case, a locally high density of beetles produces a higher catch, and, similarly, a locally low density produces a lower catch. The latter case refers to Nield's point (3.421) that a trapped beetle may act as a bait for further captures.

Table 3.1 Catch composition of experimental pitfall traps :

Pterostichus madidus.

Sex of catch	Bait:			Control:		Total Catch
	♂♂	♀♀	♂♀	New	Old	
♂	11	20	24	14	11	80
♀	4	6	3	5	5	23
Total	15	26	27	19	16	103

["New" control refers to empty, clean traps; "Old" to empty, well used traps]

Treated as 2 x 5 Contingency Table:-

catch sex ratio	:	$\chi^2 = 2.89$	($0.70 > P > 0.50$)
catch total	:	$\chi^2 = 6.08$	($0.20 > P > 0.10$)
presence of female in bait	:	$\chi^2 = 1.68$	($0.20 > P > 0.10$)
presence of male in bait	:	$\chi^2 = 1.13$	($0.30 > P > 0.20$)

In this experiment any effects due to location are minimised in order to investigate the attraction idea, with the result that no significant difference could be demonstrated between the different types of bait and traps used. However, neither was homogeneity demonstrated. The null hypothesis was neither proven nor disproven.

3.424 Conclusions

The hypothesis that captured beetles act as bait in pitfall traps was investigated, but the evidence either way was inconclusive.

3.430 Retaining Efficiency

3.431 Introduction

Having fallen into a pitfall trap, a beetle may be able to climb out again and so escape. This was clearly demonstrated when using Nebria brevicollis baits in the experiments described above (3.422). Such escapes can frequently occur if debris has fouled the trap (Gilbert, 1955), but may also be possible without such help.

A trap left in the field for a long period will eventually have its inner surfaces covered with rain-splashed mud. The smaller species of carabid readily escape if the inner surfaces are moist as the water surface tension enables them to adhere to the surface and gradually move up the walls of the trap (Mitchell, 1959; Frank, 1967; Petruska, 1969). However, this is not available for larger, heavier species (Frank, 1967; Luff, 1975). These require an irregular dry surface to grip with their tarsal claws and pads, such as rust (with metal traps), scratched surfaces (with some plastic traps), and dry rain-splashed mud (all traps). A number of authors have kept the inner surfaces of their pitfall traps clean either by regularly wiping the inner surfaces with a dry cloth, or by regularly replacing the traps

with clean ones (van der Drift, 1951; Gilbert, 1955; Mitchell, 1959; Frank, 1967; Luff, 1975). In addition, Thiele (1977) has suggested that male beetles may be more adept at climbing since they are usually smaller, and hence lighter, than the females, and are equipped with bristles on the enlarged (in many species) anterior tarsi which should facilitate climbing.

The escape potential of the different beetle species was investigated in the laboratory (3.432) and information from the field experiments described in 3.420 was examined.

3.432 Laboratory Methods

Two transparent plastic tanks were set up, each containing six of the standard jam jars used in the field as pitfall traps. To check for any humidity effect, one of these tanks was left open to the surrounding air, and the other kept moist by maintaining a few millimetres of water at the bottom of the tank and sealing the opening with a transparent plastic sheet. The tanks were kept in the laboratory throughout the study and so experienced natural day length and normal laboratory temperatures. The six pitfalls in each tank consisted of three clean and three well-used traps from the study site. Into these were placed single beetles as these became available from the Grendon Wood pitfall traps. Due to variations in catch size in this wood, the numbers used varied from day to day. Therefore the results of the experiments are given in terms of "beetle days", i.e. the product of the number of days beetles were in experimental traps and the actual number of traps involved.

Traps were examined daily for escaped beetles during the experimental period of May and June 1978.

3.433 Results and Discussion

The results (Table 3.2) clearly demonstrate that escapes were only occurring from the well-used field traps in a relatively dry atmosphere. Even the crude apparatus used to produce two different humidity situations was sufficient to demonstrate the importance of air humidity. No escapes occurred in any of the other three trap situations.

The sex ratio of the retained beetles was not found to be significantly different from that of those which escaped : all species together, $P > 0.90$; Nebria brevicollis, $P = 0.077$; Pterostichus madidus, $P = 0.47$; Abax parallelepipedus, $P = 0.74$. The results for female P. madidus and A. parallelepipedus were rather small and may not be useful. Nebria, with more results, was only just not significant at the 5% level.

The experiment does not show whether or not escape attempts occur under each condition, but that they are only successful in the relatively dry and well-used field traps. However, since all situations are very unlike the beetles' natural habitat, it seems likely that escape attempts were made in each case.

The time of day that the escapes occurred was not investigated, although daylight attempts were observed, and some were successful.

An interesting product of the experiment is the demonstration that a high proportion of the beetles can escape given the right conditions. This may indicate a far greater catch in the field than has been previously considered, but with many of the beetles escaping before the traps are examined. Of course, the laboratory beetles have

Table 3.2 Frequency of escapes of beetles from pitfall traps under different laboratory conditions

Species	Sex	Open tank						Sealed tank					
		Clean Trap			Field Trap			Clean Trap			Field Trap		
		Beetle Days	Escape Total	Beetle Days	Escape Total	Beetle Days	Escape Total	Beetle Days	Escape Total	Beetle Days	Escape Total	Beetle Days	Escape Total
<u>Nebria brevicollis</u>	♂	20	nil	17	14	16	nil	21	nil	21	nil	nil	nil
	♀	11	nil	10	5	7	nil	9	nil	9	nil	nil	nil
<u>Pterostichus madidus</u>	♂	10	nil	18	2	9	nil	19	nil	19	nil	nil	nil
	♀	-	-	8	nil	-	-	21	-	21	nil	nil	nil
<u>Abax parallelepipedus</u>	♂	33	nil	50	5	40	nil	35	nil	35	nil	nil	nil
	♀	-	-	3	nil	-	-	-	-	-	-	-	-
Total per sex	♂	63	nil	85	21	65	nil	75	nil	75	nil	nil	nil
	♀	11	nil	21	5	7	nil	30	nil	30	nil	nil	nil
Full Total	-	74	nil	106	26	72	nil	105	nil	105	nil	nil	nil

been held in captivity for some time and have no food or shelter. This might increase the "need to escape". In the field, both food and shelter may be present - having also fallen into the pitfall; and the traps are also shaded by the surrounding soil. Under field conditions, then, it may be that the escape rate will be lower. Field results need to be examined in order to answer these problems.

3.434 Examination of Field Results and Final Discussion

The loss of Nebria brevicollis beetles being used as bait in attraction experiments has already been mentioned above (3.420 and 3.431). The results of these experiments are displayed in Table 3.3.

Individually marked beetles had been placed in pitfall traps in the study site. The traps used were the existing jam jars and were not cleaned, or replaced by clean traps, during the course of the experiment. The "bait" usually consisted of two individuals, but on one occasion a single male Nebria brevicollis was used due to the lack of an available replacement following a presumed escape. Although some losses of bait beetles may have been due to predation, the high recapture rates suggest that such losses were minimal (see final column of Table 3.3).

As can be seen from Table 3.3(ii), no losses of Pterostichus madidus occurred. However, Nebria brevicollis beetles were quite adept at escaping (Table 3.3(i)), and these results have been further analysed: the figures in the "Total" column were examined for sex ratio variation by treatment as a 2 x 2 Contingency Table, producing χ^2 of 0.294 ($P > 0.30$), and indicating no significant difference between the sex ratios of retained and escaped beetles. This is comparable with the laboratory results (3.433) where no sex ratio affect could be demon-

strated, although the numbers in the present case are much larger.

The proportion of escapes from laboratory and field traps were compared (Table 3.4) and a significant difference found ($P = 0.02$), demonstrating a significantly greater loss rate under the laboratory conditions. This is not surprising considering the extreme conditions experienced here, although whether or not this is a result of escape being easier under the laboratory conditions, or that more attempts were made, is not known.

Table 3.3: Losses of bait beetles from pitfall traps in the field:

(i) Nebria brevicollis, and (ii) Pterostichus madidus

(i) Nebria brevicollis

Sex	Bait composition								Recaptures
	Two females		Two males		One of each sex		Total		
	Retained	Lost	Retained	Lost	Retained	Lost	Retained	Lost	
♂	-	-	43	10	29	3	72	13	6
♀	59	5	-	-	30	2	89	7	2
Total	59	5	43	10	59	5	161	20	8

(ii) Pterostichus madidus

Sex	Bait composition								Recaptures
	Two females		Two males		One of each sex		Total		
	Retained	Lost	Retained	Lost	Retained	Lost	Retained	Lost	
♂	-	-	80	nil	40	nil	120	nil	-
♀	80	nil	-	-	40	nil	120	nil	-
Total	80	nil	80	nil	80	nil	240	nil	-

Table 3.4: Comparison of field and laboratory results of retention of Nebria brevicollis beetles in pitfall traps (Laboratory results used here are those from well-used traps kept in a relatively dry atmosphere).

Result of Escape attempts	Laboratory results	Field results	Total
Success	19	20	39
Failure	8	161	169
Total	27	181	208

3.435 Conclusions

Glass pitfall traps continuously used under field conditions for long periods of time without cleaning have a potentially high percentage loss of catch through the captured beetles climbing out and escaping. This was found to be true for Nebria brevicollis, but apparently not for Pterostichus madidus which was found to escape only under certain laboratory conditions and in smaller numbers. Comparisons of the different sexes in this ability were inconclusive.

3.440 The effects of the time interval between capture and release

3.441 Introduction

As pitfall traps remove individuals from the population, it is desirable in population studies for the time the beetles spend in the traps to be kept to a minimum. Capture reduces the density of active beetles (Vlijm, 1961; Falk, 1974) and may also affect their behaviour following release (see also 3.350). A number of authors have left beetles in the field traps or the laboratory for long periods

before release (e.g. Greenslade, 1961; Schjotz-Christensen, 1965; Ericson, 1977), and have not considered the effects this might have on the beetles' subsequent behaviour.

It is not practical to remove, examine and release the beetles as soon as they are captured. Therefore timing effects must be investigated by increasing the length of time the beetles are held and then comparing their results with those generated when the shortest time intervals are maintained.

3.442 Methods

During the first two years of the study the captured beetles were examined and released daily except over the weekend periods when the traps were not visited at all (see Chapters 5 and 6). In addition to this, during the autumn of 1976 beetles were individually left in otherwise empty containers in the laboratory overnight on some occasions and released the following morning. Thus, a comparison is possible between individuals released the day following capture and those held either in the traps or in the laboratory overnight. In the last two cases, the beetles are separated from their normal surroundings and restrained in a small area for more than one whole activity period rather than merely a part of it as in the case of daily catch examination. Those beetles left in the traps for a second night are kept under similar environmental conditions as the uncaught beetles free in the wood, but are unable to roam at will. Food and shelter may be available if other material has fallen into the trap. Those kept in the laboratory are completely cut off from the woodland environment and have no food or shelter, but still experience the daily illumination fluctuations and, to some extent, the daily temperature fluctuations.

3.443 Results and Discussion

The aim of this section is to show whether or not an effect is present, not to produce detailed information on the precise causes and effects. Consequently the results are presented to demonstrate any effect and no further analysis is attempted.

The results for Nebria brevicollis (Table 3.5) were treated as a 2 x 4 Contingency Table using Brandt and Snedecor's Formula (in Bailey, 1964), and produced a χ^2 of 36.71 ($P < 0.001$) showing a highly significant difference between recapture rates. The five day sampling period was chosen more or less arbitrarily as a period long enough to produce sufficient recaptures but short enough to avoid having too many recovered (from any effects of captivity) beetles present. Complications due to beetles being captured, released and recaptured within the study period are also kept at a low level.

Nebria having produced such a significant result, the control figures were compared with each experimental procedure individually and treated as 2 x 2 Contingency Tables. These tests produced χ^2 statistics of 33.75 for the beetles kept in traps overnight ($P < 0.001$), 4.59 for those kept in the laboratory overnight ($0.05 > P > 0.01$), and 6.5 for those suffering both experimental conditions ($0.02 > P > 0.01$). It therefore appears that keeping beetles in field traps overnight has a highly significant effect on their subsequent recapture rate, and that keeping them in the laboratory overnight has a similar effect. The recapture rate for the "overnight trap" individuals is about 12% as compared with approximately 27% for the control individuals. Thus an effect on non-collection of Nebria brevicollis beetles over the weekend periods is to depress the recapture rate by more than one half.

Table 3.5: Nebria brevicollis, Sept - Nov. 1976 : recapture results following various procedure timings.

Trapping results after 5 days in the field	Control	Tests			Total
	Released on day following capture	In trap over-night	Laboratory overnight	Trap and laboratory overnight	
Recaptured	336	51	66	86	539
Not recaptured	919	351	250	333	1853
Total released	1255	402	316	419	2392
Recapture Percentage	26.8	12.7	20.9	20.5	22.5

(Treated as a 2 x 4 Contingency Table using Brandt and Snedecor's Formula, the recapture figures give a χ^2 of 36.71 ($P < 0.001$)

Test procedures compared individually with the control produce:

$$\chi^2 = 33.75 \quad (P < 0.001) - \text{beetles in traps overnight}$$

$$\chi^2 = 4.59 \quad (0.05 > P > 0.01) - \text{beetles in laboratory overnight}$$

$$\chi^2 = 6.5 \quad (0.02 > P > 0.01) - \text{beetles in laboratory overnight}$$

after having been left in traps
overnight

When this comparison was first started it was assumed that the laboratory-kept individuals would be the ones most likely to show a clear difference in behaviour - that the conditions here would be more "stressful". However, as far as recapture rate is concerned, the effect is quite the opposite.

The period from which the Nebria results were taken was the season of peak activity. Thus for comparative purposes the P. madidus and Abax results were also taken from their corresponding periods of peak activity. This period is the breeding season in each case (see Chapter 4). The results from outside the breeding season were too small in number to merit this form of analysis.

The results for P. madidus and Abax are presented in Tables 3.6 and 3.7. Laboratory tests were not conducted on these two species. The recapture rates were tested in the same way as for Nebria and produced χ^2 statistics of 0.4) ($0.7 > P > 0.5$) for male and 0.11 ($0.8 > P > 0.7$) for female P. madidus. The numbers of recaptured Abax were rather small and so an exact test (in Bailey, 1964) was used producing probabilities of 0.27 for male and 0.34 for female beetles. Thus for these two species, unlike Nebria, no highly significant differences in recapture rates were demonstrated. However, the recapture rates for these two species are small compared with Nebria, and firm conclusions may not be valid.

Another approach used was to examine the distances at which the recaptures were made in the five day sampling periods (Tables 3.8, 3.9 and 3.10). The higher intertrap distances have been accumulated to avoid strings of very small figures. For Nebria, each test procedure was compared with the control by treating the results as three

Table 3.6: Pterostichus madidus, May - August 1976: recapture results following different procedure timings.

Trapping results after five days in the field	♂ Beetles			♀ Beetles		
	Control	In trap overnight	Total	Control	In trap overnight	Total
Recaptured	28	11	39	13	7	20
Not recaptured	826	407	1233	336	154	490
Total released	854	418	1272	349	161	510
Recapture percentage	3.28	2.63	3.07	3.72	4.35	3.92

(Treated as 2 x 2 Contingency tables, the recapture figures for each sex give χ^2 statistics of 0.40 ($0.7 > P > 0.5$) and 0.11 ($0.8 > P > 0.7$) for male and female beetles respectively).

Table 3.7: Abax parallelepipedus, May - July 1976: recapture results following different procedure timings.

Trapping results after five days in the field	♂ Beetles			♀ Beetles		
	Control	In trap overnight	Total	Control	In trap overnight	Total
Recaptured	7	2	9	5	1	6
Not recaptured	189	81	270	92	34	126
Total released	196	83	279	97	35	132
Recapture percentage	3.57	2.41	3.23	5.15	2.86	4.55

(differences between recapture rates : male beetles $P = 0.27$, female beetles $P = 0.34$, using an exact test (after Bailey, 1964)).

Table 3.8: Nebria brevicollis, Sept - Nov 1976: displacement of recaptured beetles following various procedural timings.

Experimental procedure	Distance achieved from release point within 5 days (m.)					Total
	1	15	21/30	33	>33	
Beetles in trap overnight	26	8	6	5	6	51
Beetles in laboratory overnight	36	9	12	5	4	66
Beetles in trap, then laboratory	45	14	12	5	10	86
Control	170	53	49	28	36	336

(Treated as 2 x 5 Contingency Tables, the recapture figures produce the following statistics when each is compared with the control:-

Beetles left in field traps overnight: $\chi^2 = 0.41$ ($0.99 > P > 0.98$)

Beetles left in laboratory overnight: $\chi^2 = 2.04$ ($0.8 > P > 0.7$)

Beetles left in field traps, then laboratory overnight: $\chi^2 = 0.68$ ($0.98 > P > 0.95$)

Table 3.9: Pterostichus madidus, May - August 1976: displacement of recaptured beetles following different procedural timing. (male beetles $P = 0.25$).

Experimental procedure	Distance achieved from release point within 5 days (m.)			
	♂ beetles		♀ beetles	
	1	15+	1	15+
Control	26	2	13	nil
Beetles in traps overnight	9	2	7	nil
Total	35	4	20	nil

Table 3.10: Abax parallelepipedus, May - July 1976: displacement of recaptured beetles following different procedural timing. (male beetles $P = 0.78$, female beetles $P = 0.66$).

Experimental procedure	Distance achieved from release point within 5 days (m.)			
	♂ beetles		♀ beetles	
	1	15+	1	15+
Control	6	1	3	2
Beetles in traps overnight	2	-	1	-
Total	8	1	4	2

2x5 Contingency Tables. This produced χ^2 statistics of 0.41 (0.99 > P > 0.98) for beetles left in field traps overnight, 2.04 (0.8 > P > 0.7) for beetles left in the laboratory overnight, and 0.68 (0.98 > P > 0.95) for beetles kept in the laboratory overnight following a night left in the field trap. Thus no significant difference could be demonstrated.

The results for P. madidus and Abax were both rather small in number and an exact test was necessary for comparisons. The Contingency Table for male P. madidus produced a probability of 0.25. All females were recaptured in the same trap as they were originally captured (the release point is one metre from the trap mouth). Abax males and females produced probabilities of 0.78 and 0.66 respectively. Therefore, as with Nebria, no significant effect on displacement could be demonstrated for P. madidus and Abax.

The only significant difference demonstrated therefore is the depressed recapture rate for Nebria after being left in the traps over the weekend periods. All of these analyses concerned results achieved during the breeding seasons for the particular species. Only in Nebria are numbers of beetles sufficiently large outside this time period for a similar analysis to be made. In this species a second peak of activity occurs in the spring following overwintering. Another peak also occurs in this species in late spring and early summer - the new generation emerging from the pupae. However, this latter peak is very short for each individual and recapture rates are accordingly very small (see Chapter 4).

Analysis of the results from this spring peaks of overwintered

adult Nebria (Table 3.11) produced a χ^2 statistic of 1.41 ($0.25 > P > 0.1$) when comparing the recapture rate of the control beetles with that of those kept in the traps over the weekends. Outside the breeding season, then, no effect can be demonstrated on recapture rate. This is quite interesting. It would appear that Nebria beetles are less likely to be recaptured following a long period in the field traps only in the breeding season. But where are the beetles if they are avoiding capture? Alternative solutions are: (i) mortality, (ii) inactivity, and (iii) emigration. The last is unlikely since no significant difference was found in displacement of the recaptured beetles (Table 3.8). However, some of the figures were rather small, and strong conclusions cannot be made here.

The question of mortality is readily investigated by examining the last dates at which the Nebria beetles from each procedural category were recaptured. Only beetles first marked in the autumn of 1976 and recaptured outside that period are included to avoid the problem of multiple recaptures with multiple procedural categories. The figures are shown in Table 3.12. The figures are not directly comparable because of the exclusions but serve to show that mortality is not a major contributing factor.

The only consideration left is that of the activity levels. By a process of elimination, the depressed recapture rate of Nebria following a weekend in a pitfall trap must be due to a reduced activity level following release in the wood. However, Table 3.8 indicates that the distances achieved by the beetles are directly comparable with those of the control group. The answer must be, therefore,

Table 3.11: *Nebria brevicollis*, March - May 1976: recapture results following different procedure timings.

Trapping results after 5 days in the field	Control	Beetles in field traps overnight	Total
Recaptured	25	12	37
Not recaptured	316	98	414
Total released	341	110	451
Recapture percentage	7.33	10.91	8.20

(Treated as a 2 x 2 Contingency Table : $\chi^2 = 1.41$ ($0.25 > P > 0.1$))

Table 3.12: *Nebria brevicollis*: survival results of beetles individually marked and released during the period Sept - Nov 1976, following various procedural timings.

Release procedure	Number of individuals known to have:- (i) overwintered, (ii) and diapaused, (iii) and overwintered again			Total number re-released Sept - Nov 1976
Control	21	14	3	1255
In trap overnight	17	12	2	402
Laboratory overnight	10	7	1	316
In trap, then laboratory overnight	8	5	1	419

reduced activity of a proportion of the released beetles only. Some individuals at least, soon after release, probably burrow into the litter or soil and remain hidden for a period before resuming activity.

Greenslade (1964) described a period of disturbance dispersal for Nebria brevicollis whereby during the first 5 - 10 days after release, the amount of locomotor activity is almost twice its level afterwards. Although he only received the beetles from the traps twice a week, and kept them in the laboratory for some days before release - a situation very similar to the test procedure described above, all beetles were released at a single point in the study site, not at the recapture points of each individual as in this study. An explosive dispersal pattern is not surprising.

3.444 Conclusions

When Nebria brevicollis beetles are left in the field traps for a day or two following capture before marking and release, a short period of inactivity appears to result - at least in some of the individuals. This effect could not be demonstrated for Pterostichus madidus and Abax parallelepipedus, although the numbers of individuals in these species were rather small and may invalidate any conclusions.

Strangely, no effect could be demonstrated where the beetles were held in the laboratory overnight rather than in the field trap.

3.450 The effects of catch size on subsequent behaviour of beetles

3.451 Introduction

At high densities the competition for food and living space will be relatively great, and so individuals may need to travel

farther to satisfy their requirements, and will tend to wander into areas of lower active densities. The frequency of encounters with other individuals may therefore play an important part in determining the behaviour of a beetle. Since trapping artificially increases the density of individuals by concentrating them into a small area i.e. the pitfall trap, a density effect on subsequent behaviour may be suspected.

It is highly probable that a large catch is the result of a locally high density of individuals (see Ch. 5.320) and so any density effects may already be beginning to take affect. However, the locally high densities may be due to locally favourable circumstances and so result in the beetles remaining in the area, with consequent lowering of the activity levels - little locomotor activity is necessary to fulfil the individuals requirements.

In this section any effects due entirely to the concentrating effect of the pitfall traps are investigated. Reactions of individual beetles to their natural densities will be discussed later (Chapter 5.360).

3.452 Methods

The figures examined here are taken from the results of the pitfall trapping studies described in Chapters 5, 6 and 7, on the basis of the number of beetles of that particular species present in the original catch, and the time interval and distance achieved on the occasions of subsequent recaptures. To avoid locational and weather effects the figures for all traps and a single season are taken together and considered as a whole.

Only Nebria brevicollis is considered since the recapture rates

for the other species are too low, and the catch totals themselves contain too few large catches for such analysis.

3.453 Results

Recapture rates were considered for three groups of beetles: (i) beetles active in March and early April 1976 having survived the preceding winter (Table 3.13); (ii) those marked during the spring activity and before, and active in September 1976 (Table 3.14); and (iii) those taken first in September 1976 and therefore containing a high proportion of the new generation (Table 3.15).

In each case no significant difference could be found between the recapture rates: group (i) : $\chi^2 = 1.86$ ($0.8 > P > 0.7$), group (ii): $\chi^2 = 2.11$ ($0.9 > P > 0.8$), and group (iii): $\chi^2 = 4.36$ ($0.9 > P > 0.8$).

The next possibility to investigate was whether or not the rates of displacement of individual beetles are affected by the catch sizes. To study this the displacement rates for each of the beetles considered above were calculated. Each recapture produces two figures: the distance between the original trap of capture and the subsequent one, and also the time interval. The division of the latter into the former produces a figure for nett displacement rate. These figures were used to estimate regression coefficients which were then tested for significance.

The estimated regression coefficients (b) for the three groups of figures are -0.16 (march - April), -0.20 (September, overwintered beetles), and -0.18 (September, mostly new generation beetles), with standard errors of 0.16 in each case. None of these values for 'b' are significant at the 5% level.

Table 3.13: Recaptures of Nebria captured in March and early April 1976 (post diapause results excluded; all individuals released day following capture; $\chi^2 = 1.85$ $0.80 > P > 0.70$)

Number per trap	1	2	3	4/5	> 5	Total
Number of individuals	103	48	54	27	15	247
Number of recaptures	19	5	8	4	3	39
No. not retaken	84	43	46	23	12	208

Table 3.14: Recaptures of Nebria captured in Sept 1976, having successfully overwintered and passed through a second diapause. (post diapause results excluded; all individuals released day following capture; $\chi^2 = 2.11$ $0.90 > P > 0.80$).

Number per trap	1	2	3	4	5/8	> 8	Total
Number of individuals	9	8	10	18	9	13	67
Number of recaptures	5	4	5	13	6	8	41
No. not retaken	4	4	5	5	3	5	26

Table 3.15: Recaptures of Nebria captured in Sept. 1976 with no evidence of overwintering. (post diapause results excluded; all individuals released on the day following capture; $\chi^2 = 4.36$ $0.90 > P > 0.80$)

Number per trap	1	2	3	4	5	6	7	8/10	>10	Total
Number of individuals	102	111	84	96	50	36	38	29	38	584
Number of recaptures	54	53	42	49	29	18	23	12	18	298
No. not retaken	48	58	42	47	21	18	15	17	20	286

3.454 Discussion

In each of the three groups of Nebria brevicollis beetles the recapture rates did not significantly vary with the catch size. Indeed, the probability figures are all above 0.7 suggesting that no real difference in recapture rates exists between individuals from large or small catches. Similarly, nett displacement rates could not be shown to vary with the size of the catch.

3.455 Conclusion

Density effects created by the use of pitfall traps could not be demonstrated using the results available.

3.500 Individual marking Techniques

3.510 Introduction

The individual characteristics of ground beetles are not readily discernible to the human senses. Therefore, if the behaviour of individuals or groups of individuals is to be studied, artificial means of producing such characteristics must be devised. The technique employed must leave the animal unharmed and unaffected, and yet recognisable again on recapture (Southwood, 1966). Three approaches have been described in the literature:- (i) labelling, (ii) combinations of coloured spots of paint and dyes, and (iii) mutilation. An important aspect of all three is the handling technique employed.

Permanence of the marks is vital in a long-term study. They must remain recognisable over the whole life span of the adult beetle. If a mark is lost, then information is lost on the particular beetle and its subsequent recaptures will result in it being regarded as two individuals. This is particularly important in the case of multiple mark techniques where the loss of any one or two marks will change

the coding of an individual to that of another individual with resulting confusion of the respective recapture histories.

3.520 Labelling

The use of labels, held to the surface of animals by adhesives appears to have been used with carabid beetles only by Nield (1974). He used a liquid bituminous roofing material to fix 1mm² numbered tags onto Pterostichus madidus. Some marks survived five or six months in the field.

One problem with such marks is that the beetles push their way through leaf litter, soil and vegetation in the course of their lives and any projection from their surface is likely to catch and either slow the animal down or else fall off completely. The first affects the normal behaviour of the beetle, and the second results in loss of the information on that individual. The method is most frequently used with free flying insects such as Lepidoptera (Southwood, 1966).

3.530 Coloured paints and dyes

The application of paints and dyes to specific locations on the cuticle is a technique much practiced with carabid beetles (Drift, 1951; Mitchell, 1959; Tipton, 1960; Greenslade, 1961; Frank, 1966; Fairhurst, 1969; Mason, 1972; Baars, 1979).

Care must be taken in the choice of paints and dyes since they or their solvents may be toxic to the beetles (Southwood, 1966). The speed at which the marks dry is an important feature. Marks are easily smeared while wet either through the grooming or escape behaviour of the individuals: some may be irritant; escape attempts may

result in the beetle falling onto its back, or, if more than one individual is kept in the container, beetles may climb over each other.

Application of the paints, by pins, bristles, hairs, and so on, can be irritating to the beetles in itself.

The marks have the advantage of being visible to the human eye at distance, and so individuals can be identified and followed in the field. Thus excessive disturbance of the beetles through carriage to the laboratory for identification can be avoided (but see also 3.220). Even nocturnal species can be followed if the mark is visible in red torchlight - other wavelengths have been shown to disturb the beetles' normal activities (Gilbert, 1955; Nield, 1974).

The greatest disadvantage of the method is the lack of permanence of the marks. Many come off completely, particularly when wet (Southwood, 1966). One of the causes of this is the waxy cuticle of the beetle, which can be overcome by scraping much of it off before applying the paint spots (Murdoch, 1963; Nield, 1974).

The problem of abrasion and subsequent loss of marks through the activities of the beetles however remains. If large numbers are to be marked and released, multiple marks are necessary. This complicates things further since, unless a definite and unvarying number of spots is used on all individuals, there is no way of knowing if one or more spots have been lost (Southwood, 1966; Mason, 1972; and see also 3.510). Laboratory kept individuals have been used to study the permanence of paint marks (Frank, 1966; Pollard, 1968; Calkins, and Kirk, 1973), but it is likely that the durability under field conditions will be different since normal activity patterns may not be possible under laboratory

conditions. Paint marks have been found to be lost within a few days (Wishart et al, 1956; Rivard, 1965) and to last eight (Greenslade, 1964; Nelson, 1970) and ten months (Mason, 1972), although the latter period included five or six months when the beetle would have been hibernating. Drift (1951) concluded that, "in the long run, colour marks appeared not to be proof against the creeping in and across the litter", and this seems to be the case generally.

A further problem is increased mortality through predation in the field. Colour-marked individuals may be more obvious to predators and so have higher mortality rates than unmarked individuals. This is probably not important in the nocturnally active woodland species since light is at a very low level during their active periods and the colours will not show up very well.

An interesting variation in the use of colour marks is that of Baars (1979). All of the above description refers to pitfall trapping studies. Baars (*loc.cit.*) used ^{192}Ir -labelling to locate his individually colour-marked beetles in the field. However, the radioactivity killed most of the beetles within seven weeks.

3.540 Mutilation

Individual marking by mutilation of the beetles' cuticle has taken many forms, but generally the elytra are damaged in some way: (i) incising or notching the edges with a file or scalpel blade (Gilbert, 1955; Grüm, 1959; Nelson, 1970), (ii) punching or burning small holes - micro-cautery (Skuhravy, 1957; Schjotz-Christensen, 1961; Manga, 1972; van Dijk, 1973; Haines, 1973; Ericson, 1977^{Broncking, 1981}), or (iii) scraping away the surface cuticle between striae (Murdoch, 1963; Houston, 1969; Nield, 1974; Thomas and Sleeper, 1977) with a scalpel, razor blade, or a

rotating abrasive tip as in Houston's portable apparatus. As with paint marks, different locations on the elytra are used to represent different numbers.

Naturally mutilated beetles found in the field may produce difficulties but generally speaking artificial mutilation marks are recognisable as such. In this study some beetles were found with cracked or holed elytra and some were found to have been attacked by a parasitic mite. This mite (species unknown) left small areas of tiny marks caused by incisions of the beak into the elytron, usually in the shoulder region.

Nield (1974) mentions the possibility of mortality from entomophagous fungi after mutilation marking.

Mason (1972) found that survival of beetles with notched elytra in the laboratory was almost nil. Carabids attempted to grasp every moving object within reach, but were unable to maintain a grip on bodies of intact beetles. They could do so, however, with marked beetles and so maintain a grip out of range of the jaws of the victim. Gilbert (1955) found that notching elytra increased mortality of the beetles in the laboratory only slightly. Ericson (1977) said that microcautery appeared not to affect vitality or survival in Nebria brevicollis.

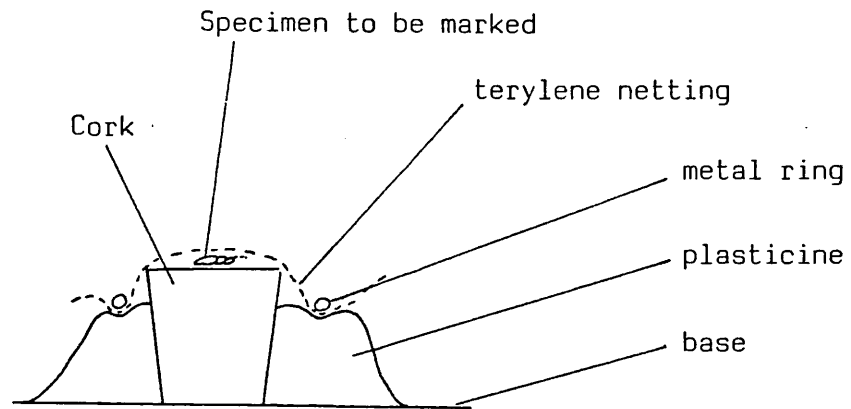
The main advantage of mutilation marking is that the marks are permanent. The wounds inflicted heal quickly but the damage is not repaired. Unfortunately immature individuals have soft elytra and cannot be marked in this way.

3.550 Handling Techniques

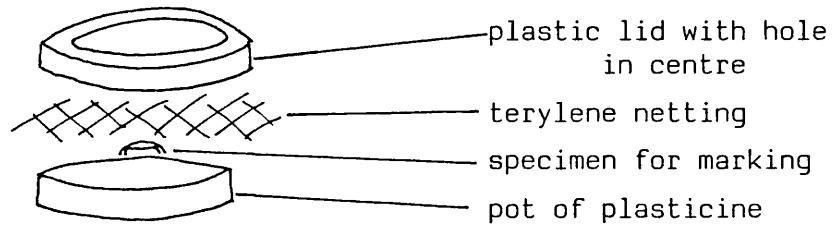
The beetles need to be still for the detailed individual marks to be applied accurately. The beetles react to touch and so need to be restrained in some way. This may be physical; with the animal held in the hand (Houston, 1969), with fine tweezers (Ericson, 1977) or beneath netting (Murdoch, 1963; Mason, 1972); or else the beetle may be anaesthetized with carbon dioxide (Gilbert, 1955; Haines, 1973; Manga, 1972) or by chilling (Southwood, 1966).

Murdoch (1963) immobilised his beetles by holding them on top of a cork by a piece of terylene net which was held taut by a ring; the ring was pushed down into plasticine surrounding the cork and the beetle marked through holes in the net. (Figure 3.1(i)). This device seems unnecessarily complicated. Mason (1972) modified this set up by replacing the cork and plasticine with a pot of plasticine and the ring by a plastic lid with a hole cut in the centre. By placing the lid over the pot with the net in between a beetle could easily be held immobile (Fig. 3.1(ii)). This was further adapted for the purposes of the present study where two pieces of card, one with a beetle-sized hole in its centre and the other intact, replace the pot and lid set up (Fig. 3.1(iii)). The beetle is held immobile with netting as in Murdoch (1963) but with the holed card acting as the ring. The pieces of card are held together by hand pressure while the mark is applied. Thus fouling of the netting with plasticine is avoided and the time of operation minimised. A series of top cards with holes of various shapes and sizes can easily be produced according to the sizes of the species to be marked.

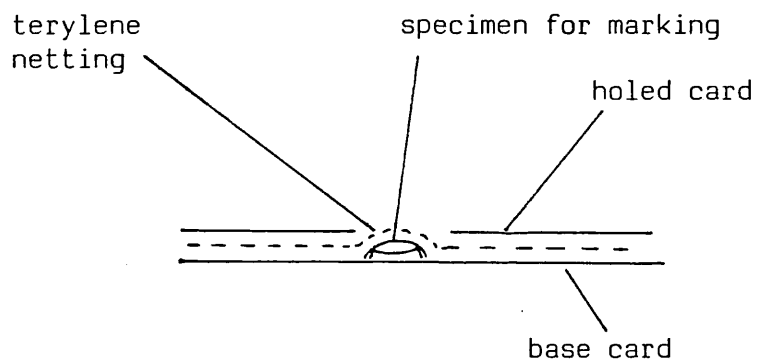
The beetle could easily be held in the hand or by tweezers for the marking process but this is a delicate business and may injure the



(i) Restraining technique of Murdoch (1963)



(ii) Technique of Mason (1972)



(iii) Technique used in this study.

Figure 3.1 Techniques used in the physical restraint of large beetles

beetle if prolonged. Houston's (1969) marking apparatus overcomes much of the difficulties of hand immobilising since it is quick and simple to use. Although this method obviates the need for taking the beetles to the laboratory for marking, this may still be necessary for ensuring accurate reading of the marks, and for determination of the sex.

The alternative approach to immobilisation, of anaesthetising the beetles, is to be avoided since it has been shown that in honey bees, not only does CO₂ cause radical changes in their behaviour (Ribbands, 1950) but also reduces their longevity (Austin, 1955). Dalmat (1950) found that female blackflies (Simuliidae) laid more eggs than normal after being subjected to CO₂. Therefore, in the absence of any investigation into the effects of CO₂ on carabids, it is far safer to find alternative methods.

Chilling has never been used to immobilise carabids, presumably because the method is time consuming, when other quicker methods are available.

3.560 Conclusions

A marking technique "must identify the animal permanently and must not affect its capacity to survive and carry out its normal functions. The marking should be quick and easy, and, to differentiate individuals, many different combinations of marks are necessary" (Murdoch, 1963). It is assumed that marked individuals are fully comparable with those unmarked.

It is evident that only mutilation techniques can fulfil all requirements, and that, of these, the scraping and burning techniques

are the more reliable since incising or notching may increase mortality. Scraping is the simplest technique and has been chosen for use in this study. The greatest dangers lie with injuries which become apparent only after a lapse of time (Dobson, 1962). This criticism has been found to be groundless in this study since long term survival after marking is commonplace (see 3.600 below).

3.600 Investigations into any effects of mutilation marking on subsequent behaviour and longevity.

3.610 Subsequent behaviour

3.611 Introduction

The beetles used in this study (Chs. 5,6 and 7) were all given individual marks using a mutilation technique based on that described by Murdoch (1963) but with a modified handling technique (Chs. 3.540 and 3.550). The marks were in the form of specific areas between the elytral striae scraped by means of a sliver of safety razor blade. Obviously a standard scrape is not possible. In practice there is a high variability of depth and area of the marks according to the sharpness of the blade, the angle of application, and the force applied. The effects of this variability were not investigated due to the complexity of such a study. However, the overall effects on the behaviour of the beetles can be studied by comparing beetles marked on the day of release with those which had been marked at some earlier capture. Thus, if it is assumed that the handling and trapping effects are equal for all individuals of one catch, the data can be analysed from this viewpoint.

3.612 Methods

Results from the main study (see Chs. 5,6 and 7) were examined and

sorted according to whether or not the individual marks were applied that day or earlier.

Problems arise from the fact that in the earlier parts of the study there are insufficient individuals with old marks. Also low capture or recapture rates or both were characteristic of all species except Nebria brevicollis.

The life history of the species must also be taken into account, including not only seasonal changes, but also survival into a second or more years of activity.

The previous sections of this chapter also need to be taken into account: beetles left in the traps or the laboratory overnight should not be included in the data (Ch. 3.440).

In order to avoid the problems, Nebria results for week days in October 1976 were used, and the "previously marked" category limited to those beetles marked within the last ten days.

3.613 Results and Discussion

Examination of the recapture rates (Table 3.16) failed to demonstrate any effect of the experience of recent scratch-marking ($P > 0.50$). Similarly the nett displacements achieved by the recaptured beetles (Table 3.17) showed no significant difference between the mark age groups ($0.30 > P > 0.20$).

3.614 Conclusion

No significant effect of marking procedure on subsequent behaviour of the beetles could be demonstrated.

Table 3.16: Nebria brevicollis, October 1976: recapture results analysed according to age of individual mark.

($\chi^2 = 0.29$, $P > 0.50$).

Mark-release results	Newly marked beetles	Previously marked beetles	Total
Recaptured	106	64	170
Not recaptured	130	88	218
Total released	236	152	388
Recapture percentage	44.9	42.1	43.8

Table 3.17: Nebria brevicollis, October 1976; recapture results analysed according to age of mark and nett displacement.

($\chi^2 = 8.91$, $0.30 > P > 0.20$)

Mark age category	Displacement achieved at recapture (m.)								Total
	1	15	21	30	33	42/45	48/53	60+	
New	33	23	7	7	11	6	8	11	106
Old	30	11	4	2	7	5	4	1	64
Total	63	34	11	9	18	11	12	12	170

3.620 Longevity

3.621 Introduction

The large numbers of beetles captured necessitated the use of multiple marking. The data for the multimark results (see Chs. 5, 6 and 7) lends itself to analysis by considering survival according to the number of marks originally applied. The problem of the variability of the scrape marks (Ch. 3.611) is assumed to be second to that due to the quantity of the marks in affecting longevity.

Laboratory studies were not undertaken because of the difficulty in separating deaths due to marking mortality from those due to poor laboratory conditions.

3.622 Methods

As in previous sections of this chapter, the data used here is derived from the main study experiments (Chs. 5, 6 and 7) and details will be found in that part of the thesis.

Since the exact dates of emergence from pupa and eventual death cannot be known with the techniques used here, longevity results are organised in terms of seasons. In the case of Nebria, beetles originally marked in (i) March and early April 1976, and having therefore already survived one winter, and (ii) September and October 1976, and assumed to contain a high proportion of the new generation, were compared on the basis of the number of marks applied to construct the individually recognisable mark code (Tables 3.18 and 3.19, respectively). Known survival through diapause or overwintering to the next season is used as the basis for comparison.

The results for other species were rather low, except in the case

of Abax, where known overwintering survival of adult beetles was examined (Table 3.20).

3.623 Results and Discussion

It is clear from the Tables (3.18, 3.19, and 3.20) that long term survival of individually mutilation-marked Nebria brevicollis and Abax parallelepipedus is commonplace. This is also true of Pterostichus madidus, P. niger, and Carabus violaceus (see Chapter 4), and, in addition, demonstrates the permanence of the marks. In each case, comparisons between individuals with differing numbers of marks were inconclusive, with the exception of overwintering survival in Nebria brevicollis (Table 3.19: $0.05 > P > 0.02$). This significant (at the 5% level) result must however be regarded as a freak chance, since the beetles with more scratch marks appeared to do better! It is unlikely that increasing the level of damage could increase the survival potential.

3.624 Conclusions

The number of scratch marks applied to the elytra of Nebria brevicollis and Abax parallelepipedus are not shown to affect the longevity of the beetles.

3.700 Release Procedure

3.710 Introduction

Both the time and location of release of animals are seldom considered important features of technique and yet both may affect the results of the experiments. Often the details of the release procedure are omitted from publications making the results far less useful.

Table 3.18: Nebria brevicollis : autumn recapture results following marking of overwintered beetles in the spring activity period. ($\chi^2 = 1.18$, $0.30 > P > 0.20$)

Autumn 1976	Number of scratch marks		Total
	Trapping results		
	2	3	
Recaptured	14	42	56
Not recaptured	54	235	289
Total released	68	277	345
Recapture percentage	20.59	15.16	16.23

Table 3.19: Nebria brevicollis : 1977 recapture results following marking of (mostly) new generation beetles in the autumn activity peak preceeding.

(overwintering survival : $\chi^2 = 4.94$ $0.05 > P > 0.02^*$

overwintering and second diapause survival = $\chi^2 = 3.05$ $0.10 > P > 0.05$)

*significant at the 5% level.

Trapping results:	Number of scratch marks		Total
	beetles marked autumn 1976		
	3	4	
Total released	478	773	1251
Recaptures March 1977	11	37	48
Recaptures Sept/Oct 1977	10	30	40
Recapture percentage March 1977	2.30	4.79	3.84
Recapture percentage Sept/Oct 1977	2.09	3.88	3.20

Table 3.20: Abax parallelepipedus : beetles known to have overwintered, analysed according to the number of constituent marks of individual mark. (i) 1976/77; (ii) 1977/78

(1976/77 $\chi^2 = 2.2$, $0.50 > P > 0.30$)

1977/78 $\chi^2 = 0.24$, $0.70 > P > 0.50$)

(i)

1977 Capture results	Number of marks applied 1976			Total
	1	2	3	
Recaptured	3	8	19	30
Not recaptured	19	139	289	447
Total released	22	147	308	477
Recapture percentage	13.64	5.44	6.17	6.29

(ii)

1978 Capture results	Number of marks applied 1977		Total
	2	3	
Recaptured	5	22	27
Not recaptured	31	177	208
Total released	36	199	235
Recapture percentage	13.89	11.06	11.49

In pitfall trapping studies the captured beetles have been removed from their natural habitat for varying lengths of time and usually subjected to laboratory examination before release. It should not be surprising to find abnormal behaviour immediately following release (Southwood, 1966), and unusually high activity levels have been described by Greenslade (1964)- see also Ch. 3.440.

Release procedure should be designed to minimise any disturbance effects.

3.720 Location of Release

This is a difficult decision. Population density estimation techniques assume equal catchability of marked and unmarked individuals (Southwood 1966). It is therefore desirable to spread the marked beetles evenly over the trapping site to achieve this, and a number of authors have followed this approach (van der Drift, 1951; Papp, 1959; Penney, 1966; Ericson, 1977). However, this may be time consuming and often the release of all marked beetles in the centre of the grid is used as a more convenient alternative (Mitchell, 1959; Dempster et al, 1959; Greenslade, 1961; Coaker and Williams, 1963; Rivard, 1965; Grüm, 1971; Manga, 1972; Calkins and Kirk, 1973).

In studies of local movements of individuals the beetles should be placed as near the trap of origin as possible. Obviously releasing by the trap may bias the recapture results due to beetles immediately falling back into the trap. Haines (1973) released his beetles at a metre from the trap and this seems a useful distance. Other authors released the marked beetles near the trap but give no precise distance information (Wishart et al, 1956; Tipton, 1960; Grüm, 1962, 1965¹⁹⁸¹; Mason, 1972; Nield, 1974; Thomas and Sleeper, 1977^{Rijnsdorp, 1980; Brunsting, 1981}) or else released them

midway between the trap of origin and a neighbouring one (Rickard et al, 1965; Nelson, 1970).

One of the aims of this study is to look for sedentary species, which, incidentally, invalidate the use of estimation techniques. These may associate with particular locations in the site and so it is essential to replace them where found. If a beetle has a home range, its behaviour will be affected far more if released outside that range than if released inside it.

3.730 Time of Release

If the beetles are wanted to behave normally as soon after release as possible then obviously they should not be left in the traps or the laboratory any longer than is strictly necessary for examination and marking (see Ch. 3.440).

In addition, the time of day of the release is also important. If the species has a marked periodicity of locomotor activity, then it should be released during its inactive period (Southwood, 1966). Hence the period between the disturbance and full activity is lengthened, minimising the possibility of escape reactions taking the individuals away from the site. In the case of the nocturnal woodland ground beetles, release is preferable during the daylight hours.

3.740 Conclusions

In order to avoid excessive disturbance of the beetles, they should be returned as soon as possible, and during their inactive period, close to the point of capture within the study site.

3.800 Summary of Chapter

Methods available in the study of movements of individual ground

beetles under field conditions are discussed, and in certain cases further investigated.

Capture techniques are discussed and pitfall trapping selected as the most suitable for the present study. Sources of variation in catch size and composition are also discussed, and the following considerations investigated experimentally:

- (i) The possibility of active aggregation of beetles in pitfall traps - results inconclusive.
- (ii) Retaining efficiency - a potentially high percentage loss of captured beetles through escape was demonstrated in Nebria brevicollis, but not in the larger, more heavily-built, Pterostichus madidus.
- (iii) The effects of the time interval between capture and release on subsequent behaviour in the field - a significant drop in re-capture rate of Nebria brevicollis beetles was found following release if the beetles were left in the field traps ^{or the laboratory} for a day or two following capture. This affect could not be demonstrated for Pterostichus madidus or Abax parallelepipedus, although the numbers of individuals in the last two species were too small for valid comparisons.
- (iv) The effects of catch size on subsequent behaviour of the beetles - density effects created by the concentrating effect of pitfall traps could not be demonstrated.

Individual marking techniques are discussed and a modification of Murdoch's (1963) scratch-marking technique selected for use in this study. Effects of this technique on subsequent behaviour and longevity

of beetles were investigated but none could be demonstrated.

Release procedures are discussed, and it is concluded that excessive disturbance should be avoided by returning the beetles as soon as possible, and during their inactive period, close to the point of capture within the study site.

Chapter 4
Life histories of the commonest
larger woodland Carabidae

4.100 Introduction

Although all Carabidae large enough to receive a recognisable individual mark were given one, only five species were common enough, and were recaptured in sufficient numbers to make analysis of the results worthwhile (see Chapters 5, 6 and 7).

Details of the life histories of the five will be considered in this chapter.

4.200 Nebria brevicollis

First instar larvae were pitfalled from October until April, second instar from November until April, and third instar from November to May (Table 4.1). The third instar was by far the most frequent in traps, with peak catches in January, February and March. Immature adults, recognisable by their soft cuticle and, occasionally, paler colouration, were recorded in May and June, and three specimens also in September 1976. During July and August very few beetles were captured, but activity was again resumed by early September, reaching a peak in October before trailing off through the winter months. Numbers in traps again began to increase in the spring, reaching a peak in March before the new generation of adults emerge (see also Figure 4.1).

This outline life history is in agreement with previous studies of this species (Gilbert, 1958; Williams, 1959b; Greenslade, 1965; Penney, 1966; Thiele, 1969; Evans, 1969; Houston, 1970; Manga, 1972; Haines, 1973; Nield, 1974; Luff, 1975^{),} ^{Dennison et al., 1984; Kalas, 1985} and the small variation may be accounted for by meteorological and climatical effects. The species is clearly seen to fit into Thiele's (1977) third life history category as a species with winter larvae and adults which emerge in

Table 4.1: Monthly catch totals of *Nebria brevicollis*. (Mature adult totals adjusted to catch per 500 trap days for comparative purposes: "Product of trap days" is the product of the number of traps and the number of days when they are open).

	J	F	M	A	M	J	J	A	S	O	N	D
1975 Mature adults										118	102	92
Total adjusted to 500 trap days										641.3	261.5	117.7
Callow adults												
Larvae: Instar III											1	8
" " II											1	7
" " I												
Product of trap days										92	195	391
1976 Mature adults	32	96	285	164	89	38	2	11	1257	1668	238	38
Adjusted totals	37.5	49.5	56.2	67.6	23.1	7.7	0.7	2.0	468.0	391.0	46.5	8.19
Callow adults					29	14			3			
Larvae: Instar III	35	177	235	52	2						2	15
" " II	8	15	55	5							29	42
" " I	9	14	6							13	37	20
Product of trap days	427	969	2537	1214	1925	2478	1520	2804	1343	2133	2560	2320

Continued

Table 4.1: (Continued)

	J	F	M	A	M	J	A	S	O	N	D
1977 Mature adults	23	23	18	5	41	68	5	412	955	241	28
Total adjusted to 500 trap days	4.6	5.1	4.7	2.6	7.5	12.6	0.8	647	150.6	50.2	12.4
Callow adults					53	8					
Larvae: Instar III	124	150	43	5	1					2	27
" " II	45	26	13	2						3	5
" " I	34	5	2							6	
Product of trap days	2480	2240	1920	960	2744	2700	2970	3185	3170	2403	1129
1978 Mature adults	17	27	44	19	33	86					
Adjusted totals	2.76	6.1	9.0	4.5	11.2	23.2					
Callow adults					73	22					
Larvae: Instar III	373	635	788	202	6						
" " II	26	34	30	2							
" " I	13	4	1	1							
Product of trap days	3081	2212	2449	2130	1472	1856					

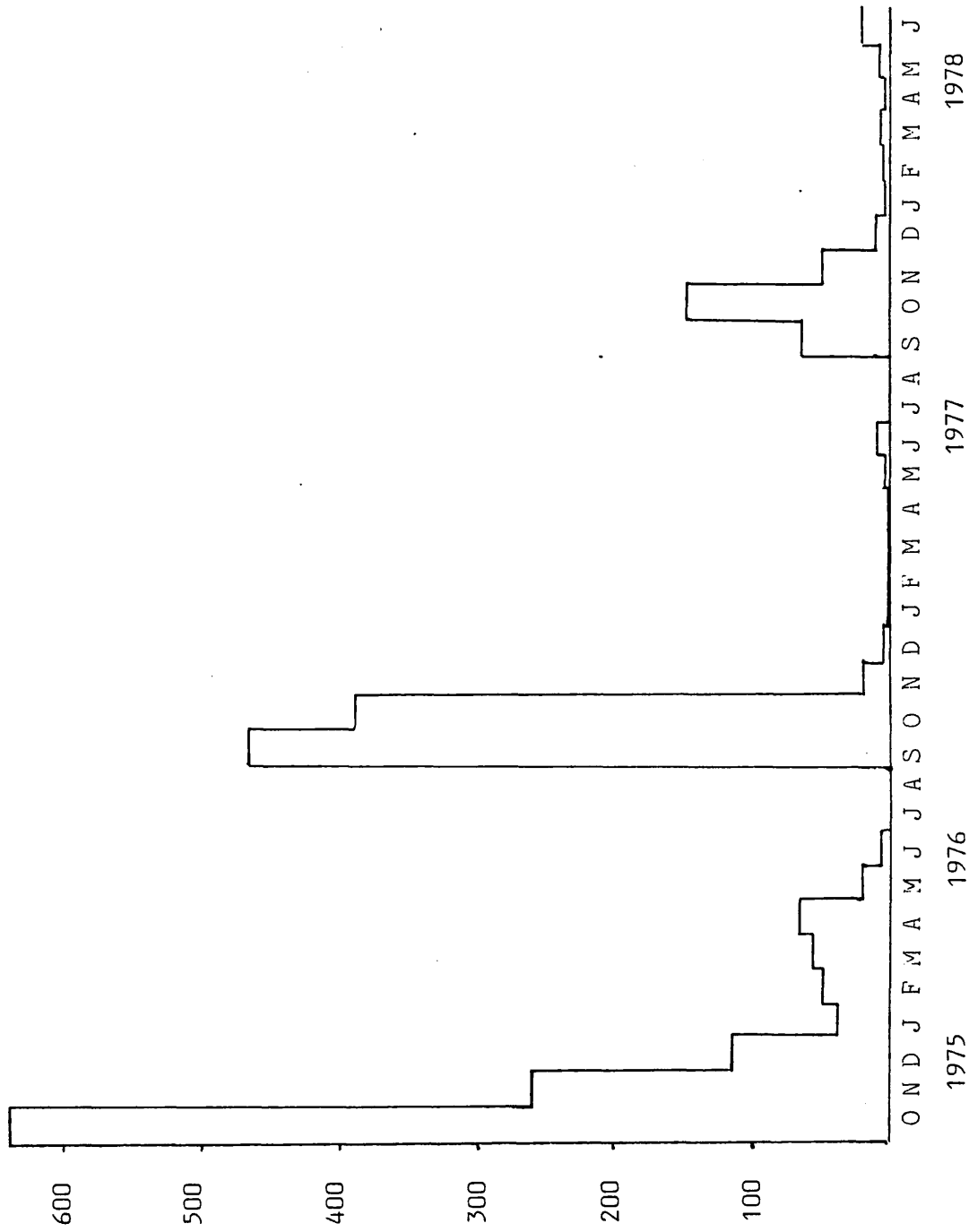


Figure 4.1 : Monthly adjusted trapping totals for *Nebria brevicollis* (mature in colour and cuticle hardness)

[N.B. peak heights not directly comparable due to the variation in trap totals and locations used]

the spring, and undergo aestivation prior to reproduction in the autumn. Many adults survive the winter, and later breed for a second time in the following autumn (see Ch. 5).

The presence of apparently immature individuals in small numbers in September has been recorded by other workers (Greenslade, 1965; Muggleton, 1970; Haines, 1973; and Luff, 1975). The length of time needed to achieve mature colouring is given as 20 days by Greenslade (*loc.cit.*), and so the immature beetles must be presumed to have emerged from the pupal stage in August. Luff (*loc.cit.*) has shown that eggs laid in March will not have reached the pupal stage until the latter half of August, and so will produce an immature adult in the autumn. Unfortunately, none of these individuals has been dissected to examine the condition of the reproductive organs, but it is clear that Luff's suggestion is the most reasonable solution.

In Figure 4.1 the results have been adjusted to catches per 500 trap-days sampled, and only beetles with mature colouring and hard cuticle included. The horizontal scale is too contracted to show that, in fact, there are three peaks in adult activity each year. Examination of the adult beetle catch totals in Table 4.1 shows that after the main peak in activity of September - October, there is a second peak of overwintered beetles becoming active in the spring, and a third of the new generation emerging and becoming active in late spring and early summer. Marking results (see Ch. 5) show that the two spring peaks are entirely separate. This is precisely as described by Gilbert (1958) where, by the time the new generation become active, the overwintered beetles have already become inactive, presumably as they enter aestivation for a second time. Individual marking (Ch. 5)

clearly shows that some of these beetles survive into a second breeding season, and some still are present in subsequent breeding seasons.

A few individuals were captured during the July - August aestivation period. Ganagarajah (1964) and Anderson (1972) state that movement during the summer period of inactivity may be merely a shifting of aestivation site, and hence of restricted movement. As Anderson (*loc.cit.*) points out, it is most advantageous to respond to disturbance during aestivation and to immediately seek another place to hide, otherwise predation is likely.

Two inactive, and presumably diapausing individuals were found outside the study area in July and August: one female was found deep in a mass of tree roots in a garden; and another individual was found beneath an empty chemical drum on wet ground in an oak-alder copse.

A number of authors have examined the change in sex ratio through the year. Greenslade (1965), Penney (1966) and Nield (1974) found that the sex ratio was approximately 1:1, but, in addition to this, the activity levels of the sexes varied with season. Greenslade (*loc.cit.*) and Nield (*loc.cit.*) found that males were more active in the breeding season, although Penney (*loc.cit.*) found that the females were more active immediately after aestivation. Nield (*loc.cit.*) also found that females were more active in the winter months and that more of them survived the winter. Penney (*loc.cit.*) also found that immature males were more active initially than females.

Examination of the Great Wood seasonal capture figures for December 1977 until July 1978 shows that only during the winter of 1978 did females predominate over males in the pitfall traps (Table 4.2).

Table 4.2: Nebria brevicollis: change in sex ratio of trapped beetles with season (initial difficulties in separating sexes has resulted in not all trapped beetles being included).

Season	Calendar months	Males	Females	♂/♀ Ratio
Winter	Dec-Feb 1977	24	8	3.00
Spring (overwintered adults)	Mar-Apr.	17	6	2.83
Late Spring (new generation)	May-July	96	73	1.32
Autumn	Sept	243	168	1.45
	Oct	682	290	2.35
	Nov	170	73	2.33
Winter	Dec-Feb 1978	25	47	0.53
Spring (overwintered adults)	Mar-Apr.	47	29	1.62
Late Spring (new generation)	May-July	125	87	1.44

However, in the autumn the prevalence of males was least, agreeing to some extent with the findings of Penney (loc.cit.). There was no evidence that females survived the winter in greater numbers, as suggested by Nield (loc.cit.). Indeed the spring ratios suggest the opposite. It seems more likely that the females are more active in the winter months due to some of them still seeking oviposition sites - as mentioned above, egg laying can continue well into the new year. It is possible that Nield's (loc.cit.) actograph studies gave a spurious result due to the beetles' surroundings being uniform and uniformly unsuitable for oviposition.

Some individuals were dissected throughout the year (Tables 4.3 and 4.4). One female captured in February or March 1976 still carried a mature egg, but all others were spent. The new generation showed no development of reproductive organs. Females entering their second breeding season were found to exhibit very dark corpora lutea as compared with those of the newly ovipositing new generation. Thus, the remains of the trophic cells of the previous season are retained in this species. This makes separation of the two age groups fairly easy early in the autumn, although the distinction gradually becomes obscured as oviposition continues. Corpora lutea from more than one year's breeding cannot be separated into age groupings by eye, although the work of Heerdt et al (1976) suggests that it may have been possible using optical aids.

Some larvae were collected from the field and reared in the laboratory, partly to confirm identity, and partly to examine timing and characteristics of the moults (Table 4.5).

Table 4.3: Results of dissections of female Nebria brevicollis beetles at various time of the year. (unmarked beetles)
 *species with an unsegmented parasitic worm filling abdominal cavity.

Capture period	Callow females	Gravid females (number of eggs found)		Spent females
		Corpora lutea		
		pale	dark	
Feb-Mar 1976			1	4
Apr-May				3
June-Jly	4			
Sept		7,4,9,17,7	12,4	
Oct			21,18,7,8,20	
Nov		*	1,52,5,15,7,6,6	
Jan 1977			16,3	
Apr-May	1			
Sept		19,15,11,19,19,7, 18,11,2,3		3
Nov			13,7,19,13,12, 23,21	1
Dec		*	4	1
Jan 1978		*,7	5	1
Feb				3

Table 4.4: Results of dissections of marked *Nebria brevicollis* females at various time of the year.

Capture dates	Final date	Condition of reproductive system on date of last capture	Individual reference mark
1976: Apr 14	Sept 27	Corpora lutea dark; 2 large eggs	606
1976: Sept 21, 25	Sept 27	5 large eggs	921
1976: Sept 17	Sept 27	Corpora lutea dark; 19 large eggs	801
1976: Apr 14, Sept 25, Oct 6,	Oct 11	Corpora lutea dark; 7 large eggs	601
1976: Sept 14, Oct 7	Oct 19	8 large eggs	747
1976: Sept 14	Oct 25	Corpora lutea dark; 24 large eggs	719
1976: Sept 30, Oct 6	Oct 19	Corpora lutea dark; 4 large eggs	1269
1976: Oct 5, 11	Oct 27	2 large eggs	1452
1976: Oct 11	Nov 1	Corpora lutea dark; 15 large eggs	1613
1976: Oct 25, Nov 1, 5,	Nov 8	Corpora lutea dark; 13 large eggs	1924
1976: Sept 20, 27, Oct 4,	Nov 8	18 large eggs	830
1976: Oct 28, Nov 8,	Nov 17	10 large eggs	1951
1976: Dec 6	1977: Jan 5	Corpora lutea dark; 10 large eggs	1/242
1976: March 29, Apr 12, Sept 16, Sept 20, 27, Oct 4, 8, Nov 1,	1977: Jan 10	Corpora lutea dark; 7 large eggs	436
1977: Sept 10, Oct 24,	Nov 2	Corpora lutea very dark; 18 large eggs	1/427
1977: Oct 7	Nov 8	Corpora lutea very dark; 20 large eggs spent	1/799
1976: Oct 12	1977 Oct 10, 24,		1706
1976: Oct 18	1977 Oct 12, 14, 20, Nov 10	Corpora lutea dark; 21 large eggs	1827

Continued..

Table 4.4: (Continued)

Capture dates	Final date	Condition of reproductive system on date of last capture	Individual reference mark
1977: Sept 9,	Nov 11	Corpora lutea dark; 19 large eggs	1/412
1977: Sept 28	Nov 11	Corpora lutea dark; 3 large eggs	1/621
1977: Sept 30, Oct 24, Nov 11,	Nov 15	2 large eggs	1/673
1977: Oct 14, 24, Nov 10,	Nov 29	spent	1/894
1977: Sept 26, Oct 24,	Nov 29	4 large eggs	1/531
1977: Oct 14, 24	Nov 29	18 large eggs	1/896
1977: Oct 21, Nov 14,	Nov 29	Corpora lutea very dark; 12 large eggs	1/982
1977: Sept 26, 27, 30	Nov 29	20 large eggs	1/526
1977: Oct 4, 14	Dec 29	1 large egg	1/738
1977: Oct 24	Dec 29	spent	2/334
1977: Oct 19	Dec 29	Corpora lutea very dark; 20 large eggs	1/941
1977: Oct 19	Dec 29	Corpora lutea very dark; 23 large eggs	1/944
1977: Dec 29	1978: Feb 2	spent	2/478
1977: Oct 19	1978: March 13	spent	1/949

Table 4.5: Results of laboratory rearing of *Nebria brevicollis*

Capture date	Moult dates				Comments
	Instar I→II	II→ III	III→ Pupa	Pupa → Adult	
17 Feb 1976			8 March		larva writhing 4 March
17 Feb 1976			4 March		succumbed to fungal disease
2 Apr. 1976			7 April		succumbed to fungal disease
10 Jan 1977			7 Feb	14 Feb	died partly emerged
23 Feb		10 March			
23 Feb			10 March	21 March	♀, pale colour; mature colour 4 Apr.
23 Feb	10 March				
6 Apr.		12 April			
4 May			12 May	20 May	larva writhing 9-11 May
27 Feb 1978			9 March		larva writhing 7 March
27 Feb 1978			9 March	20 March	larva writhing 7 March
28 Feb			9 March		larva writhing 7 March
27 Feb			13 March		
27 Feb			13 March		
27 Feb			13 March		writhing 7 March
27 Feb			*		larva of parasitic wasp emerged and pupated 13 March
28 Feb			*		larva of parasitic wasp emerged and pupated 20 March

4.300 Pterostichus madidus

First instar larvae were trapped from September until January, second instar from October until May, and third instar from November to June (Table 4.6). Immature adults were present from May until September, reaching a peak (in 1976) in August, although the capture records of this stage is variable from year to year. As with Nebria brevicollis, mature adults were present all year round, with greatest pitfall catch from May until August. Again, overwintering of adults is common, since the peak in activity begins before the main peak in immature beetles. This is also confirmed by marking studies (Ch. 5), which also demonstrate that survival into a second, third, and even fourth breeding season occurred (Ch. 4. 820).

This life history fits Thiele's (1977) second category with adults breeding in the summer and autumn, and producing winter larvae, and is in accordance with published life history studies (Williams, 1959b; Briggs, 1965; Greenslade, 1965; Houston, 1970; Mason, 1972; Luff, 1973; Haines, 1973; and Nield, 1974).

Overwintering in adults of this species is well known (Drift, 1959; Greenslade, 1965; Briggs, 1965, etc.) and they are found deep in the soil at this time. The reproductive organs of the spent beetles become productive again in the following season, and are probably responsible for the earlier larvae (Luff, 1973), since these adults emerge some months before the new generation of adults. It has been suggested that most of the overwintered adults do not breed in the previous season (Greenslade, 1965; Haines, 1973). However, Luff (1973) could find no evidence that the overwintering females did not oviposit in the previous year. The fact that some adult beetles overwinter on more than one occasion indicates that breeding in more

Table 4.6: Monthly catch totals of Pterostichus madidus (Mature adult totals adjusted to catch per 500 trap days for comparative purposes; "Product of trap days" is the product of the number of traps and the number of days when they were in use).

	J	F	M	A	M	J	J	A	S	O	N	D
1975 Mature adults										16	31	12
Total adjusted to 500 trap days										87.0	79.5	15.4
Callow adults												3
Larvae: instar III												1
Larvae: instar II											2	1
Larvae: instar I										92	195	391
Product of trap days												
1976 Mature adults	2	25	108	180	603	859	282	489	29	82	72	5
Adjusted totals	2.3	12.9	21.3	74.1	156.2	173.3	92.8	87.3	10.8	19.0	14.1	1.2
Callow adults					3	3	37	78	1		6	2
Larvae: instar III	2	13	41	48	24	13						
Larvae: instar II	12	24	14	2	1						2	2
Larvae: instar I	6									45	49	3
Product of trap days	427	969	2537	1214	1925	2478	1520	2804	1343	2133	2560	2320

Continued..

Table 4.6: (Continued)

	J	F	M	A	M	J	J	A	S	O	N	D
1977 Mature adults	5	6	26	23	259	200	76	232	98	182	41	5
Adjusted totals	1.0	1.3	6.8	12.0	47.3	37.0	35.2	39.1	15.4	28.7	8.5	22
Callow adults					4			1				
Larvae:instar III					1						2	11
Larvae:instar II	1									4	51	3
Larvae:instar I									3	6	2	
Product of trap days	2480	2240	1920	960	2744	2700	1080	2970	3185	3170	2403	1129
1978 Mature adults	5	5	18	70	340	306	22	7				
Adjusted totals	0.8	1.1	3.7	16.4	115.6	82.4	69.2	29.2				
Callow adults							47	59				
Larvae:instar III	19	5	20	31	7	1						
Larvae:instar II	12	3	2	1								
Larvae:instar I												
Product of trap days	3081	2212	2449	2130	1472	1856	159	120				

than one season is probable, and this is confirmed by dissections (see Tables 4.8 and 4.9).

One immature female beetle which appeared very late in 1976 was dissected (Table 4.8) and the ovaries found to be very small and covered by a tight mesh of tracheae, and were obviously immature. Being immature in November, this individual is likely to have not bred that season. Thus the overwintering adult population does contain a few individuals which have not previously bred, and is therefore a mixture of young unbred and spent individuals.

Kowalski (1974) and Nield (1974) found a peak in activity in the autumn and suggested that this consisted of adults feeding up prior to hibernation. A suggestion of this is seen in both the 1976 and 1977 pitfall catches where the September catches were lower than in October (see Table 4.6 and Figure 4.2).

Some authors have examined the change in sex ratio of beetles in the pitfall traps over the year. Females were captured in greater numbers in the spring (Greenslade, 1945; Evans, 1969; Luff, 1973; Kowalski, 1974; Nield, 1974), and this has been explained as greater overwintering survival of the females. Greenslade (*loc.cit.*) found that, while the proportion of mature to immature females in the autumn was about 3:1, the ratio was reversed by early May. He concluded that most of the winter mortality fell on the spent individuals, and that overwintering beetles were mainly those which had not bred in the previous season (see above). This is contradicted by studies of the reproductive organs taken in conjunction with individual marking, where evidence is found that breeding in a second season is fairly common (see Tables 4.8 and 4.9).

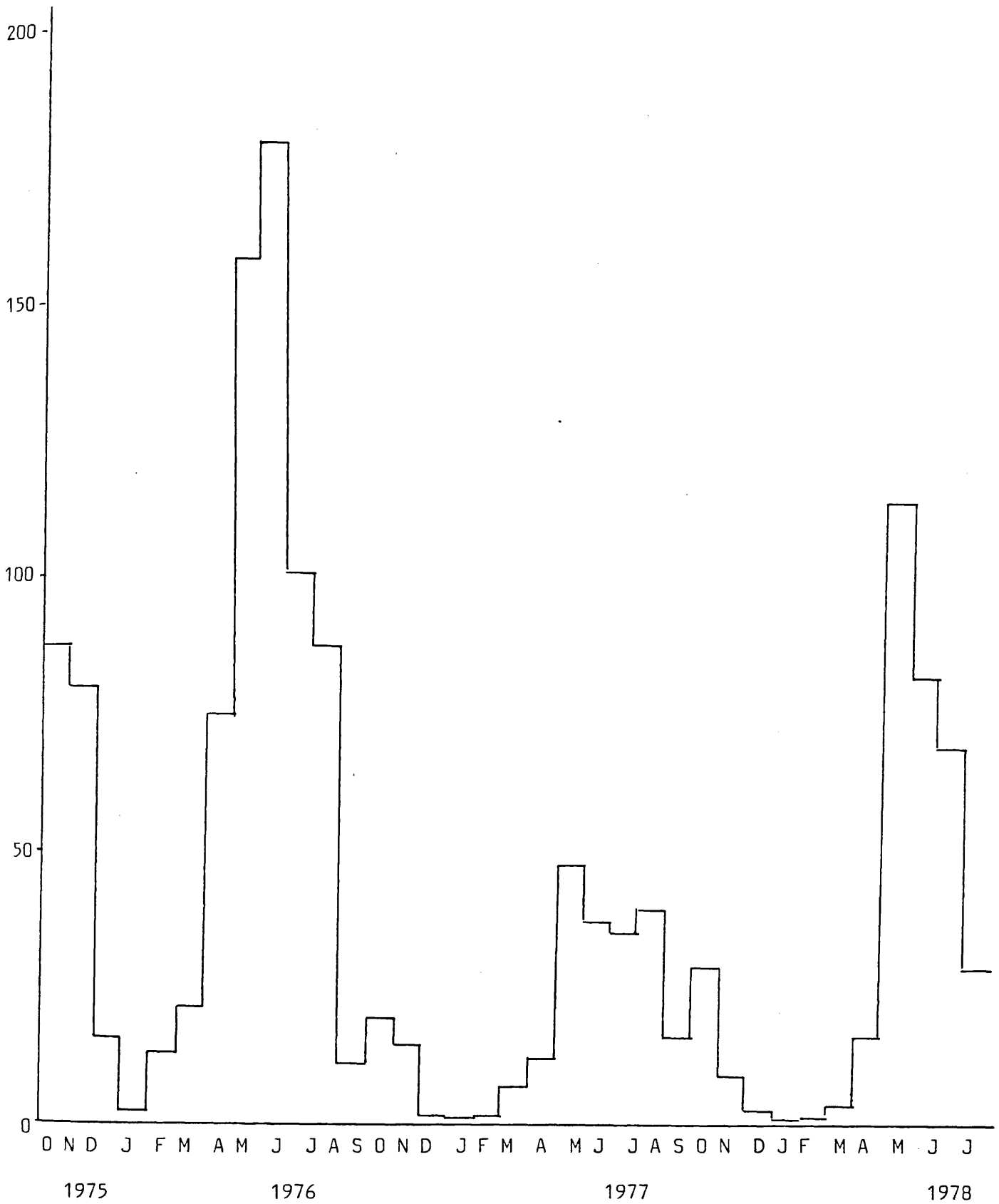


Figure 4.2 Monthly adjusted trapping totals for *Pterostichus madidus* (mature
in colour and cuticle hardness)

[N.B. peak heights not directly comparable because of the variation in total traps and locations used]

The sex ratio approaches equity as the main activity period gets underway and the new generation emerges (Greenslade, 1965; Luff, 1973), and eventually reaches the point where males are more commonly captured as the breeding season gets underway (Dempster, et al, 1959; Greenslade, 1965; Luff, 1973; Nield, 1974). After this the majority of the males die according to Greenslade (1965), with only a few surviving into the autumn. However, Kowalski (1974) and Luff (1973) both found that many males survive the winter and become active again in the following season, although in smaller numbers than the females.

The Great Wood monthly catches are separated according to sex in Table 4.7. The changes in sex ratio over the year follow that previously described. In the spring females predominate, but the ratio reverses over May and June, and males are pitfalled in greater numbers in July and August. The ratio again reverses in September, and females again predominate into the autumn and winter months. That many males survive the winter can be clearly seen from the figures: many hundreds of males were active in the spring of 1976 before any callow adults were captured. Indeed, in this spring, they outnumbered the overwintered females in the pitfall traps, although in the following two years females did predominate.

Here again the confusion between activity and abundance becomes evident (see 3.352). The predominance of females in traps in autumn and winter must reflect their greater activity then, as compared with the males. This, in fact, is shown in Nield's (1974) actograph studies. He found that the females were more active than males, particularly in the latter part of the year. This was the reverse of his field pitfall catch figures. Actograph studies should, however, be

Table 4.7: *Pterostichus madidus* : change in sex ratio of trapped beetles over the year.

(i) Cuticle hard (mature adults)

Month	1975		1976		1977		1978		
	Males	Females ♂/♀ ratio	Males	Females ♂/♀ ratio	Males	Females ♂/♀ ratio	Males	Females ♂/♀ ratio	
J			2	nil ∞	nil	5	0	1	4 0.25
F			17	8 2.13	2	4	0.5	nil	5 0
M			69	39 1.77	12	14	0.86	6	12 0.5
A			81	99 0.82	5	18	0.28	21	49 0.43
M			219	384 0.57	50	209	0.24	46	294 0.16
J			653	206 3.17	107	93	1.15	168	138 1.22
J			252	30 8.4	56	20	2.8	15	7 2.14
A			382	107 3.57	198	34	5.82	7	nil ∞
S			21	8 2.63	45	53	0.85		
O	2	14 0.14	27	55 0.49	12	170	0.07		
N	nil	31 0	4	68 0.06	5	36	0.14		
D	2	10 0.2	nil	5 0	nil	5	0		
Total	4	55	1727	1009	492	661		264	509

Continued..

Table 4.7 (Continued)

(ii) Cuticle soft (immature adults)

	1976		1977		1978	
	nil	nil	nil	nil	nil	nil
J-M	nil	nil	-	-	nil	nil
A	nil	1	0	-	nil	nil
M	nil	3	0	2	nil	nil
J	1	2	0.5	-	nil	nil
J	16	21	0.76	-	33	14
A	31	46	0.67	0	43	16
S	nil	1	0	-	nil	nil
O	nil	nil	-	-	nil	nil
N	nil	6	0	-	nil	nil
D	nil	2	0	-	nil	nil
Total	48	82		2	2	76
						30
						2.36
						2.88

interpreted with caution as pointed out in 4.200.

Some individuals were dissected throughout the year (Tables 4.8 and 4.9). Corpora lutea were visible in only two old females. Luff (1973) reported something approaching this situation, and Dawson (1957) found the same in other Pterostichus spp. and Agonum spp. This unfortunately means that the majority of overwintered females entering another breeding season could not be distinguished from the new generation, the Corpora lutea usually being lost when the second batch of eggs are laid. One female captured in November 1977 had small undeveloped ovaries that were densely tracheated. This is probably a late emerging individual of the new generation and would have first produced eggs in the following year. Another female in the same month was found to contain two large eggs as well as sixteen, pale white, small eggs. The Corpora lutea were visible in this specimen, and it must be assumed to be producing a second batch of eggs. Luff (1973) thought it likely that most females produce only a single batch of eggs in one season. This specimen is then an exception. Copulation was observed on eleven occasions from June 21 until September 23 (see Table 4.21).

Some larvae were collected and reared in the laboratory (Table 4.10).

Laboratory kept beetles were frequently found to have constructed shallow burrows in the soil in which they spent the daylight hours, and others were found at the bottom of the container under the 5cm depth of soil. Occasionally these latter beetles could be seen to be inside a small cell excavated into the soil. Such cells and burrows were found throughout the year in the laboratory soil containers, although

Table 4.8: Results of dissections of female Pterostichus madidus, all previously unrecorded in grid.

Capture period	Reproductive system undeveloped	Gravid females (number of eggs found)	Spent females
March-May 1976		1,3,11,2,1	8
June-July	2	29,3,4,18,20,12,10,21	2
August	6	3,6,28,2,10,9,13,6,18 3(small), 28,12	
Sept		7,16	2
Oct		1,5	10
Nov			6
Apr-May 1977			7
June		15	
August	2	18,4,19,20	
Sept		4,1,1	7 (Corpora lutea visible in one)
Oct		1,8,11	
Nov	1 (ovarioles small and densely tracheated)	5,2,21g + 16 small (dark Corpora lutea)	4
Feb 1978			1
March			
April		15	5
May			15
June	4	8,6,7,16	

Table 4.9: Results of dissections of marked Pterostichus madidus females, and recapture history.

Capture dates: final date	Condition of reproductive system on date of last capture	Individual re- ference mark
1976: May 12, May 26	1 large egg	537
1976: June 9, Aug 30	2 large eggs	929
1976: July 26 (soft cuticle) Aug 30	13 large eggs	1/282
1976: Oct 8, Nov 8	Spent	1/841
1976: Nov 5 1977 Oct 17	1 large egg	1/903
1977: May 12, Oct 20	Spent	2/375
1977: Oct 2,6, Oct 24	Spent	3/454
1977: Aug 31, Dec 21, 1978 Jan 11	Spent; Corpora lutea visible	2/966
1978: May 11, June 9	Undeveloped	3/820
1978: May 31, June 15, June 20	6 large eggs	3/943

Table 4.10: Results of laboratory rearing of Pterostichus madidus larvae (N/K refers to changes not observed)

Capture date	Moult dates				Comments
	Instar I → II	→ III	→ Pupa	→ Adult	
13 Feb 1976	18 March	9 June	18 June	18 June	♀ larva writhing 7 Apr; ♂
12 Feb		9 April	23 April	23 April	♀
17 Feb		17 May	2 June	2 June	♀
18 Feb		N/K	9 June	9 June	♀
29 Dec 1977		18 April	2 May	2 May	♀
20 Feb 1978		18 April	1 May	1 May	♀
7 April		N/K	17 May	17 May	♀
7 April		N/K	28 May	28 May	♂
3 May		2 June	12 June	12 June	♀
21 April		25 June			died

the former predominated in winter.

4.400 Abax parallelepipedus

No first instar larvae were pitfalled during the three year study period, and only five second instar - in May (1), September (2), October (1), December (1), but third instar larvae were taken in every month of the year except August, with two peaks : May - June, and a smaller one in the autumn (Table 4.11). Immature adults similarly showed two peaks roughly synchronous with those of the third instar larvae, whereas only a single activity peak was found for mature adults : April to October (see also Figure 4.3).

The life history of this species is obviously complex. It has been investigated by a number of authors (Greenslade, 1965; Fairhurst, 1969; Evans, 1971; Mason, 1972; Haines, 1973), but none in any detail. Consequently it is but poorly understood. Thiele (1977) placed it in his fourth reproductive grouping, where the reproductive period is flexible : both spring and autumn reproduction occurring in a single year, and the larvae develop equally well under summer and winter conditions. However, adults and larvae are much less tolerant of winter conditions than the preceding two species, and spend the period inactive. Kowalski (1974) found adults down to 20cm, and larvae usually at greater depths, in cells in the soil during late autumn and winter. This, together with the flexible breeding season and short surface activity period, makes the interpretation of the pitfall results rather difficult.

The main complicating feature in the life cycle is the flexible breeding season. Drift (1951) found that overwintered females produce mature eggs two weeks after emerging from hibernation. Therefore,

Table 4.11: Monthly catch totals of Abax parallelepipedus. (Mature adult totals adjusted to catch per 500 trap days for comparative purposes; "Product of trap days" is the product of the number of traps and the number of days when in use).

	J	F	M	A	M	J	J	A	S	O	N	D
1975 Mature adults												
Total adjusted to 500 trap days												
Callow adults												
Larvae: instar III												
Larvae: instar II												
Larvae: instar I												
Product of trap days										92	195	391
1976 Mature adults												
Adjusted totals												
Callow adults												
Larvae: Instar III												
Larvae: Instar II												
Larvae: Instar I												
Product of trap days	427	969	2537	1214	1925	2478	1520	2804	1343	2133	2560	2320

Continued..

Table 4.11: (Continued)

1977 Mature adults	J	F	M	A	M	J	J	A	S	O	N	D
Total adjusted to 500 trap days	1	2	1	3	55	70	29	111	16	4		
Callow adults		0.5	0.3	1.6	10.0	13.0	13.4	18.7	2.5	0.6		
Larvae: instar III	1				1				1		4	2
Larvae: instar II												1
Larvae: instar I												
Product of trap days	2480	2240	1920	960	2744	2700	1080	2970	3185	3170	2403	1129
1978 Mature adults			1	9	133	250	33	25				
Adjusted total			0.2	2.1	45.2	67.4	103.6	104.1				
Callow adults					1	1						
Larvae: Instar III	2	1	1	1	1	1						
Larvae: Instar II												
Larvae: Instar I												
Product of trap days	3081	2212	2449	2130	1472	1856	159	120				

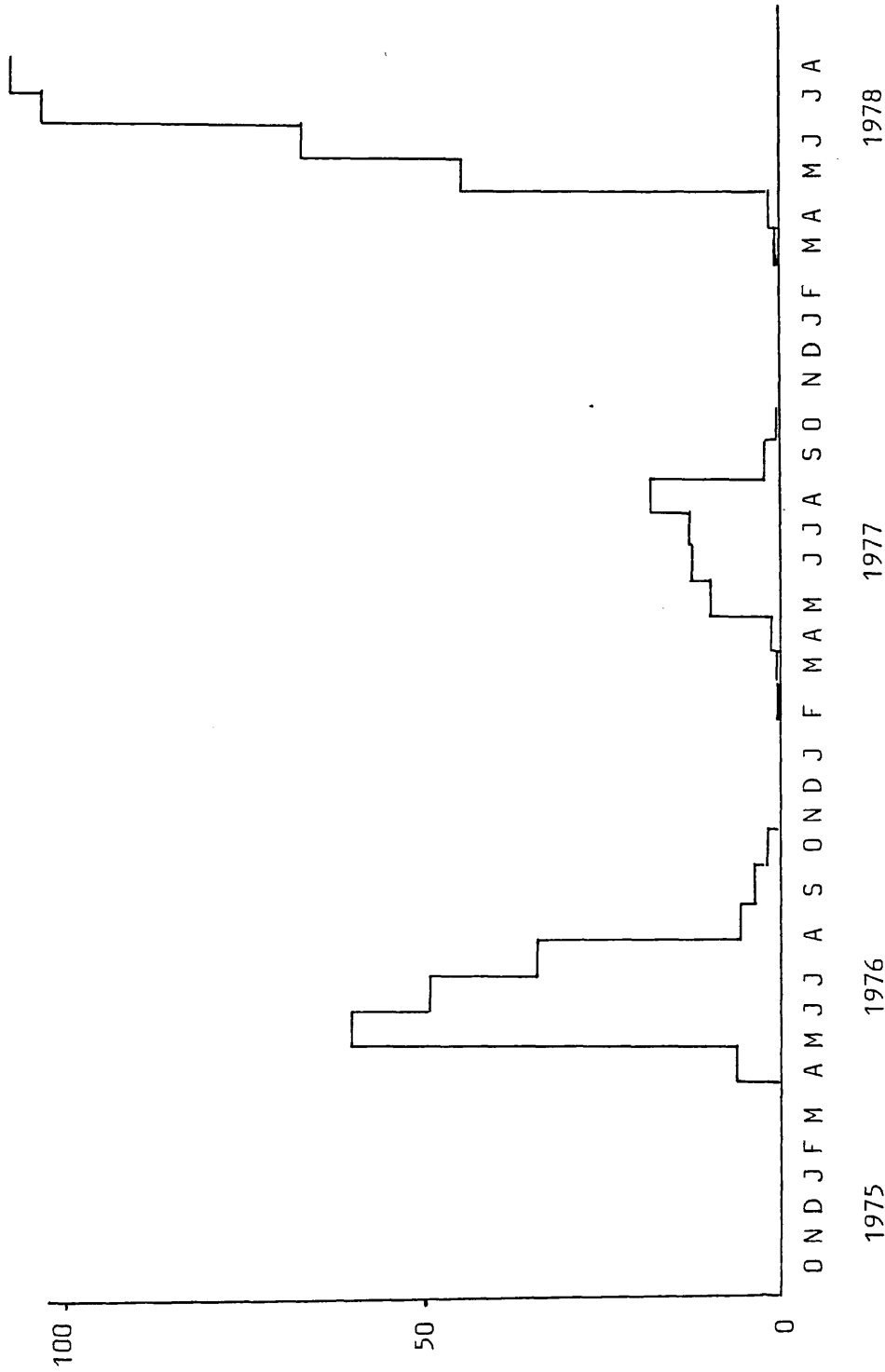


Figure 4.3 Monthly adjusted trapping totals for Abax parallelepipedus (mature in colour and cuticle hardness)

[N.B. peak heights are not directly comparable because of the variation in total traps and locations used]

overwintered females will be ovipositing from May onwards. Copulation has been observed throughout the summer activity period (Greenslade, 1965; Haines, 1973; and see Table 4.21), with only a single peak in July (Haines, loc.cit.). Early eggs hatch and produce first instar larvae in July and August which overwinter as the third instar, and pupate in the spring to produce the early peak in immature adults (see Figure 4.4: Larval Cycle 1). However, eggs laid later in the season either overwinter in that stage or as first and second instar larvae. Drift (1951) found first instar larvae as late as October and November. These will not have reached the third instar by the onset of winter. Therefore larvae will be present during the following summer, and will pupate and produce the late peak of immature beetles, which in turn overwinter before breeding for the first time (Figure 4.4: Larval Cycle 2). The second cycle requires two years for completion, as suggested by Frank (1966) and Houston (1970), and so is similar to the fifth life history category of Thiele (1977) known to occur in the closely related Abax ovalis Dufts (Lampe, 1975).

Larval Cycle 1 results in adults which will first breed and oviposit late in the following year, and therefore gives rise to eggs which follow Larval Cycle 2 (see Fig. 4.4), but these adults may successfully overwinter and produce eggs early in the following season. These eggs will follow Larval Cycle 1. Larval Cycle 2 results in adults emerging too late in the year to breed and oviposit before winter, and so results in Larval Cycle 1. Hence the two cycles are very interrelated. Although the basic conclusion that there are two concurrent cycles has been described by the previous workers, the interrelationships seem to have been missed. The proposed life cycle based on the above description is illustrated in Figure 4.4. Climatological

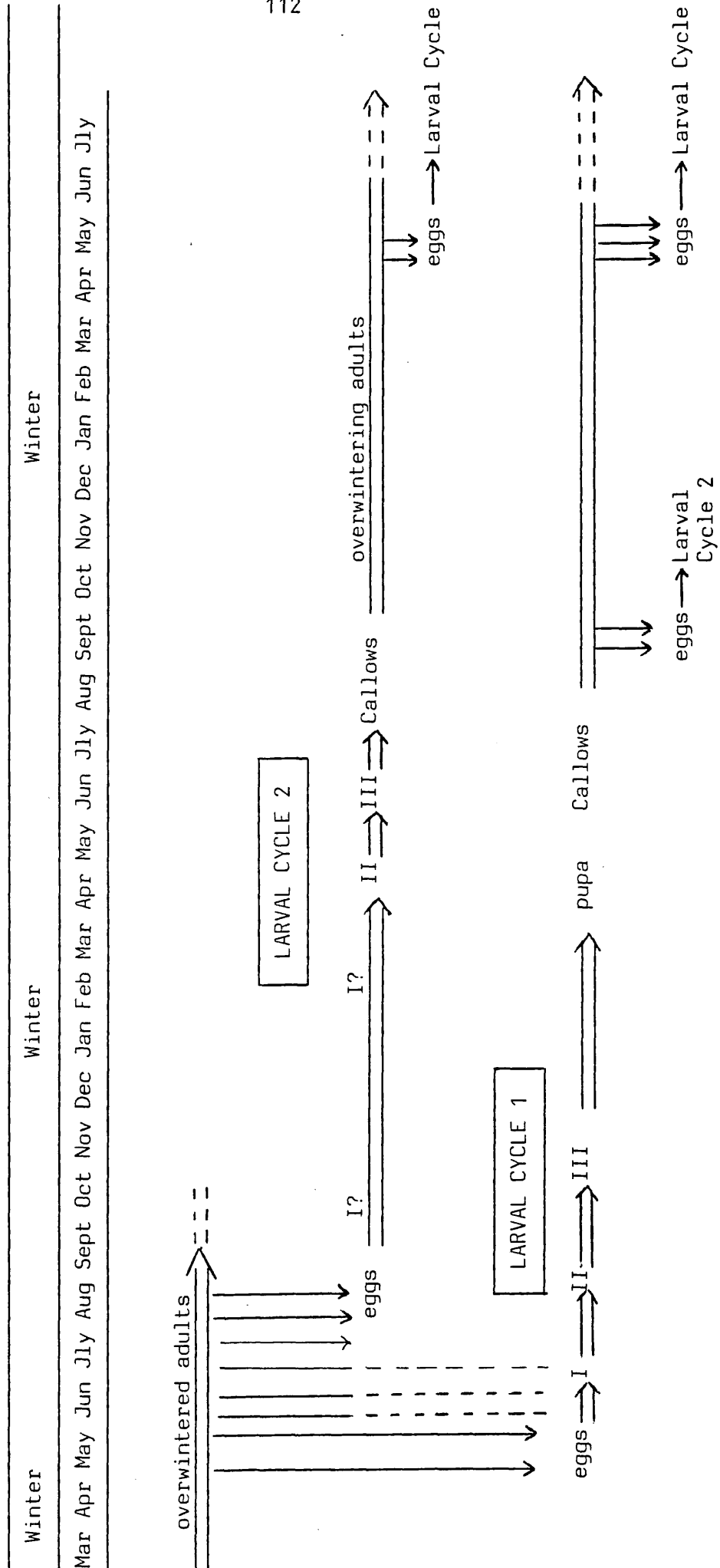


Figure 4.4 Proposed life cycle for *Abax parallelepipeda*

effects on the ability of each cycle to proceed will be important. For example, at colder latitudes the activity period of the species will be shorter and all eggs will produce Larval Cycle 2 (see Houston, 1970 for example) since Cycle 1 requires a longer summer period.

Drift (1951) and Greenslade (1965) found that male beetles were dominant early in the season and females later. The Great Wood results are analysed by sex in Table 4.12. It is immediately evident that male activity predominated all year round, and no late female activity was observed.

The results of dissecting female beetles are shown in Tables 4.13 and 4.14. It is interesting to note the presence of large eggs in April, 1976. These beetles must have carried the eggs throughout the winter inactivity period. Corpora lutea could not be distinguished in any of the dissected beetles and so age categories could not be determined.

No Abax larvae were successfully reared in the laboratory, which is strange considering their flexibility in the field.

Adults maintained in containers in the laboratory regularly constructed burrows, indistinguishable from those of Pterostichus madidus except in size, although less commonly than that species.

4.500 Carabus violaceus

This species, like Abax, has a restricted period of activity in this country : adults were captured from May until September, with a peak in July - August. Immature adults were common in June and July, 1976, but absent in 1977, and only a single specimen in 1978 (June).

Table 4.12: Abax parallelepipedus: monthly change in sex ratio.

Month & Year	Mature Beetles			Callow Beetles		
	Male	Female	♂/♀ ratio	Male	Female	♂/♀ ratio
1976						
Jan-Mar	nil	nil	-	nil	nil	-
Apr	5	10	0.5	nil	1	nil
May	133	90	1.48	11	8	1.38
Jun	171	76	2.25	6	8	0.75
Jly	70	26	2.69	1	nil	∞
Aug	20	13	1.54	12	5	2.4
Sept	10	1	10	10	12	0.83
Oct	5	4	1.25	6	8	0.75
Nov	nil	nil	-	nil	1	nil
Dec	nil	nil	-	nil	nil	-
1977						
Jan	nil	nil	-	nil	1	nil
Feb	2	nil	∞	nil	nil	-
Mar	nil	1	nil	nil	nil	-
Apr	2	1	2	nil	nil	-
May	38	17	2.24	nil	1	nil
Jun	45	25	1.8	nil	nil	-
Jly	18	11	1.64	nil	nil	-
Aug	74	37	2	nil	nil	-
Sept	7	9	0.78	nil	nil	-
Oct	2	2	1	nil	nil	-
Nov-Dec	nil	nil	-	nil	nil	-
1978						
Jan-Feb	nil	nil	-	nil	nil	-
Mar	1	nil	∞	nil	nil	-
Apr	7	2	3.5	nil	nil	-
May	89	44	2.02	1	nil	∞
Jun	177	73	2.42	1	nil	∞
Jly	25	8	3.13	nil	nil	-
Aug	25	2	12.5	nil	nil	-

Table 4.13: Results of dissections of female Abax parallelepipeda, all previously unrecorded in the grid.

Capture period	Reproductive system undeveloped	Gravid females (number of eggs present)	Spent females
1976: Apr	1	18,15,14	1
June-Aug		7,3,4,6,2,5,10,4,10,2,8,5	2
Sept	1		5
1977: Apr-May		1	
Jun		10,6	
Aug 1-22		11,3,1	1
Aug 23-31		5,1,1	2
Oct			2
1978: Apr	1		
May	1	7,8,3,4	1
June		13,11,6,10	

Table 4.14: Results of dissections of marked female Abax parallelepipedus, and recapture history.

Capture dates	Condition of reproductive system on date of last capture	Individual reference mark
1978: May 23 Jun 20	15 large eggs	765
Jun 10 Jun 23	14 large eggs	846
Jun 12 Jun 28	3 large eggs	854
May 28, Jun 9, Jun 29	16 large eggs	778
Jun 17 Jun 29	7 large eggs	866

Larvae, all third instar, were only recorded in autumn 1977 (Sept - November) with a peak in October, and were, therefore, only present in the year when no immature adults were found (Table 4.15)

A detailed study of this species in Britain has yet to be published. First instar larvae have been recorded in July and August, second from September until December, and third similarly from September to December. Immature adults have been recorded in May and early June, and have matured by late June and July, when breeding takes place (Houston, 1970; Haines, 1973). Adults frequently overwinter (Greenslade, 1965), and this can be seen in Table 4.15, and both sexes were involved (see Table 4.16), although marking only demonstrated overwintering in females (see Ch. 5). In Figure 4.5

Table 4.15: Monthly catch totals of Carabus violaceus 1976-78 in Great Wood (Mature adult totals adjusted to catch per 2000 trap days for comparative purposes; no adults or larvae were captured Oct - Dec 1975; "Product of trap days" is the product of the number of traps and the number of days in use).

1976 Mature adults	J	F	M	A	M	J	J	A	S	O	N	D
Total adjusted to 2000 trap days			3		3	2.4	22	21	2			
Callow adults			3.1		20	37	15.0	3.0				
Larvae: instar III												
Larvae: instar II												
Larvae: instar I												
Product of trap days	427	969	2537	1214	1925	2478	1520	2804	1343	2133	2560	2320
1977 Mature adults					4	12	9	32	2			
Adjusted totals			2.9		8.9	16.7	21.6	1.3				
Callow adults												
Larvae: Instar III									1	15	1	
Larvae: Instar II												
Larvae: Instar I												
Product of trap days	2480	2240	1920	960	2744	2700	1080	2970	3185	3170	2403	1129

Table 4.15 (Continued)

	J	F	M	A	M	J	J	A	S	O	N	D
1978 Mature adults								9				
Total adjusted to 2000 trap days							75.5	1.50				
Callow adults						1						
Larvae: instar III												
Larvae: instar II												
Larvae: instar I												
Product of trap days	3081	2212	2449	2130	1472	1856	159	120				

Table 4.16: Carabus violaceus : monthly change in sex ratio.

Month & Year	Mature Beetles			Callow Beeles		
	Male	Female	♂/♀ ratio	Male	Female	♂/♀ ratio
1976: May	1	2	0.5	nil	nil	-
Jun	1	1	0.5	13	6	2.17
July	10	12	0.83	14	16	0.88
Aug	10	10	1	nil	nil	-
Sept	1	1	1	nil	nil	-
1977: May	nil	4	nil	nil	nil	-
Jun	5	7	0.71	nil	nil	-
July	4	5	0.8	nil	nil	-
Aug	6	25	0.24	nil	nil	-
Sept	1	1	1	nil	nil	-
1978: Jun	nil	nil	-	nil	1	nil
July	1	5	0.2	nil	nil	-
Aug	5	4	1.25	nil	nil	-

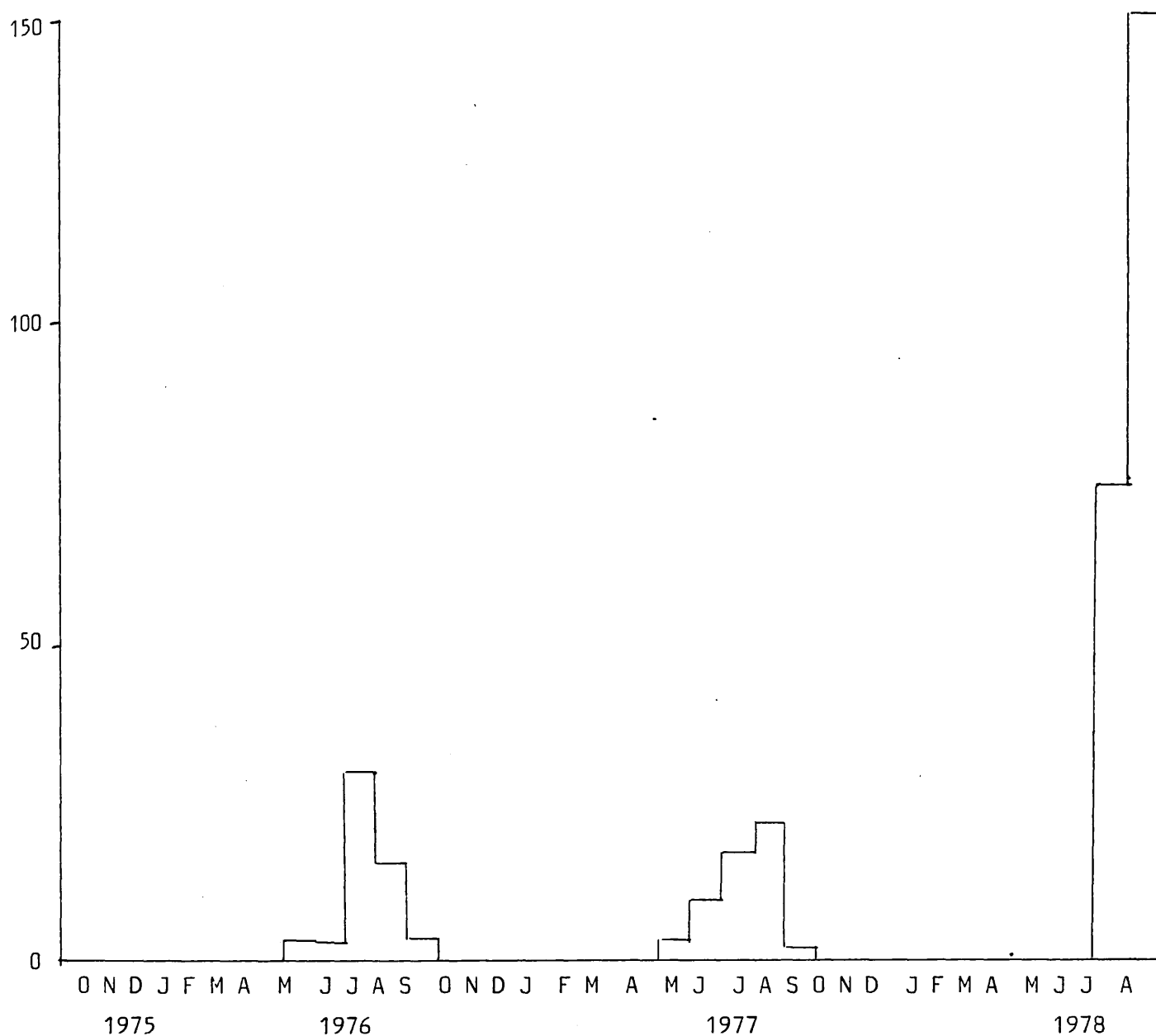


Fig. 4.5 Monthly adjusted totals for *Carabus violaceus* (mature in colour and cuticle hardness)

[N.B. peak heights are not directly comparable because of the variation in total traps and locations used]

the results have been adjusted to catches per 2000 trap days sampled, and only beetles exhibiting full maturity in external feature included.

The life cycle as described above is similar to that of Pterostichus madidus, but with the activity cycle more restricted by the climate.

Greenslade (1965) noted that the first adults to emerge in the late spring were overwintered females. These were followed later by the males before the emergence of the new generation. The sex ratios found in Great Wood are given in Table 4.16. A few individuals were captured early in the season and both sexes were represented, although in 1977 only females were taken in the first month of capture. The females predominated overall in each year, even though in 1976, more callow males were taken than females. This, together with the fact that all marked individuals found to have overwintered were female, recalls a study by Fabre (1911) where female Carabus auratus Linn. eviscerated all males they came across at the end of the breeding season. Thus one would expect to find overwintered males in much lower numbers than females in that species. In mid August 1978 one of the females in a laboratory soil tank containing two females and one male, did in fact eviscerate the male.

No larvae were reared successfully in the laboratory. Due to the smaller numbers of individuals of this species in the pitfall traps, few were kept for dissection (Table 4.17). Adults kept in the laboratory in soil containers constructed shallow burrows in the soil beneath loose pieces of wood, in which they spent the daylight hours.

Table 4.17: Results of dissections of female *Carabus violaceus*

Capture period	Reproductive system	Gravid females (number of eggs present)	Spent females
1976 Jun-Aug	undeveloped		
1977 Aug 23-31	2	4 large plus many small	

4.600 Pterostichus niger

Monthly catch totals for this species are shown in Table 4.18. The figures show little deviation from published life histories: third instar larvae were trapped in October, January, February and May, and immature adults in July and August. Mature adults were found from March until September, and exceptionally in November, and thus overwintering of adults is again common. Following low numbers in 1976, a dramatic increase in activity was observed in 1977, and there were signs that this was continuing in 1978. Thus 1976 appears to have been an exceptionally bad year for this species (see also Figure 4.6 and Ch. 2.500).

Some information on this species is present in the literature (Larsson, 1939; Drift, 1951; Greenslade, 1965; Grüm, 1973; Haines, 1977; Jorum, 1980), but, as with Carabus violaceus and Abax parallelepipedus, no detailed study has yet been made in Britain.

Grüm (1967) found the sex ratio to be even in Polish forests. Examination of the Great Wood figures (Table 4.19) shows a slight preponderance of male beetles early in the season (March - May) which balances out towards the peak in breeding activity.

Only two larvae were reared successfully in the laboratory, both from third instar to adult, and both emerging on the 20th May (one of each sex). A number of females were dissected and the condition of the ovarioles noted (Table 4.20).

4.700 Field Observations

1977: May 4 Pterostichus niger ♂ found beneath the bark of a dead coppiced oak stool, 60cm above the soil surface. Midday, Great

Table 4.18: Monthly pitfall capture totals for Pterostichus niger. (Mature adult totals adjusted to catch per 2000 trap days for comparative purposes; no adults or larvae were captured Oct-Dec 1975, and only third instar larvae elsewhere; "Product of trap days" is the product of the number of traps and the number of days in use).

	J	F	M	A	M	J	J	A	S	O	N	D
1976												
Mature adults			3	1	9	11	12	14	3			
Totals adjusted to 2000 trap days			2.4	1.7	9.4	8.9	15.8	10.0	4.5			
Callow adults							2	1				
Larvae:Instar III					1					1		
Product of trap days	427	969	2537	1214	1925	2478	1520	2804	1343	2133	2560	2320
1977												
Mature adults					5	10	10	229	92		1	
Adjusted totals					3.6	7.4	18.5	154.2	57.8			
Callow adults												
Larvae:Instar III												
Product of trap days	2480	2240	1920	960	2744	2700	1080	2970	3185	3170	2403	1129
1978												
Mature adults					3	27	22	18				
Adjusted total					4.7	29.2	278.5	300				
Callow adults								1				
Larvae:Instar III	3	2										
Product of trap days	3081	2212	2449	2130	1472	1856	159	120				

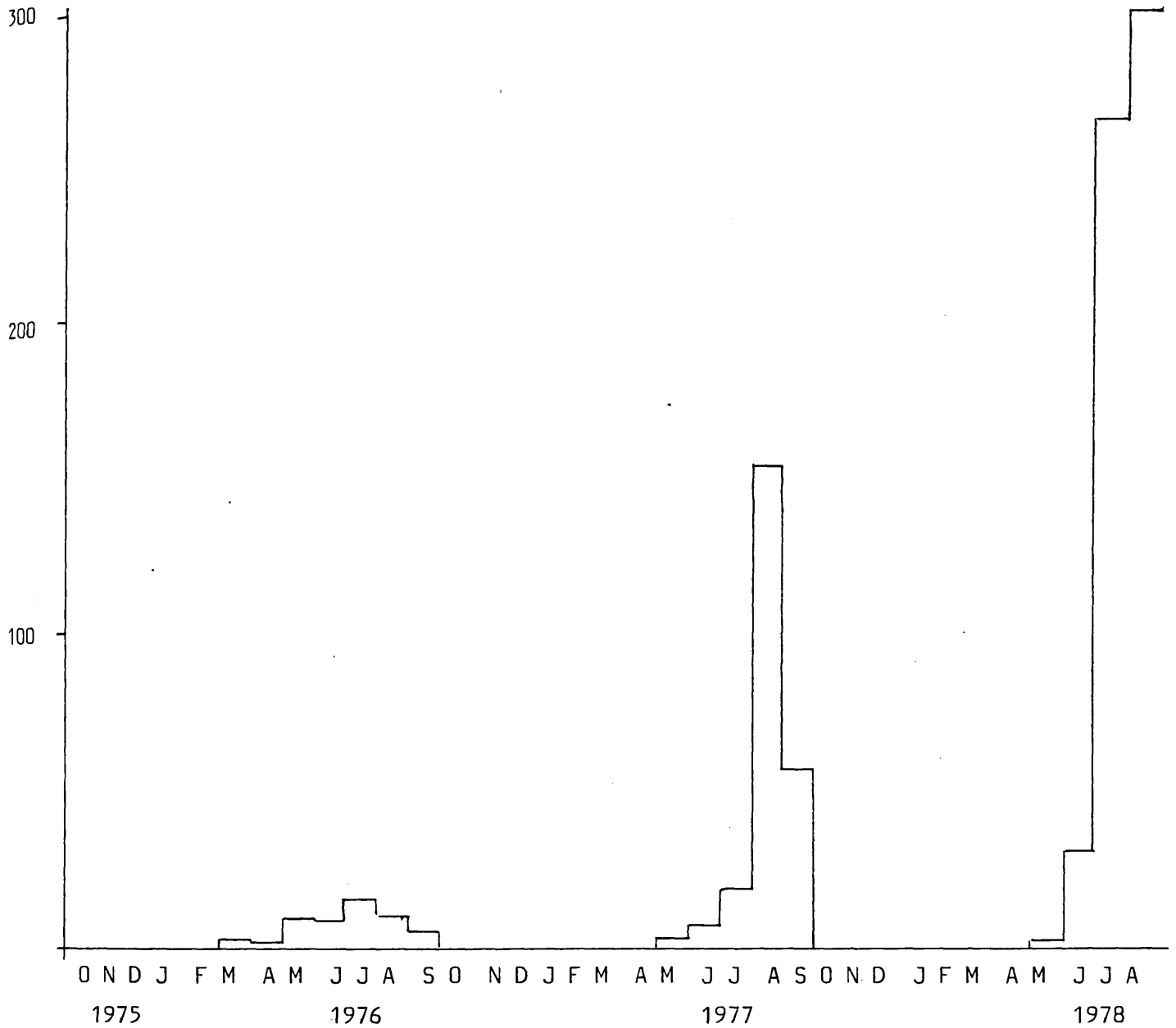


Figure 4.6 Monthly adjusted totals for *Pterostichus niger* (mature in colour and cuticle hardness).

[N.B. peak heights are not directly comparable because of the variation in total traps and locations used]

Table 4.19: Pterostichus niger: monthly change in sex ratio.

Month & Year	Mature Beetles			Callow Beetles		
	Male	Female	♂/♀ ratio	Male	Female	♂/♀ ratio
1976 March	2	1	2	nil	nil	-
Apr.	1	nil	∞	nil	nil	-
May	6	3	2	nil	nil	-
Jun	5	6	0.83	nil	nil	-
July	8	3	2.67	nil	2	nil
Aug	8	6	1.33	nil	1	nil
Sept	2	1	2	nil	nil	-
1977 May	5	nil	∞	nil	nil	-
June	5	5	1	nil	nil	-
July	3	7	0.43	nil	nil	-
Aug	118	111	1.06	nil	nil	-
Sept	38	54	0.70	nil	nil	-
Oct	nil	nil	-	nil	nil	-
Nov	nil	1	nil	nil	nil	-
1978 May	3	nil	∞	nil	nil	-
Jun	9	18	0.5	nil	nil	-
July	7	15	0.47	nil	nil	-
Aug	8	10	0.8	1	nil	∞

Table 4.20: Results of dissections of female *Pterostichus niger*.

Capture period	Reproductive system undeveloped	Gravid females (number of eggs present)	Spent females
1976: June		2,16,5	
1977: Aug 1-22		9,5,7,1,9,9	2
23-31		8	
Sept		5,15,15	
1978 June		22,24	

Wood.

July 23 Nebria brevicollis ♀ found inside the root mass of an Ailanthus tree sucker in garden at Ham, Surrey. Midday.

Aug 17 Nebria brevicollis beneath an old chemical drum on wet ground beneath rhododendron bushes in an oak-alder copse in the grounds of the Zoology Department, R.H.C. 2.00pm.

1978: April Nebria brevicollis third instar larva found in a burrow in the compacted soil of a footpath in Great Wood - pupated a few days later.

April 14 Pterostichus madidus ♀ walking over the leaf litter surface in Great Wood, 10.10am.

May 10 Nebria brevicollis ♀ callow individual running over leaf litter in Great Wood, 10.20 am.

June 26 P. madidus ♂ found beneath leaf litter, on the soil surface, in Great Wood, 2.30pm.

October 14 Nebria brevicollis running across footpath along the edge of Grendon Wood, 4.20pm.

On a number of occasions beetles were found to be copulating in the field pitfall traps (Table 4.21). All of these observations were during the daylight hours. This raises the question of the location of mating activity under true field conditions. Do the beetles mate on encountering each other while foraging? or only while in the daytime refuges? Mating beetles have been observed to remain in copuli for a number of hours. This impairs mobility to some extent, and will therefore increase the chances of predation. It would seem beneficial to the beetles concerned if mating took place in a refuge.

Table 4.21: Dates when copulation observed.

Year	<u>P. madidus</u>	<u>A. parallelepipedus</u>	<u>N. brevicollis</u>
1976:	Aug 20		Oct 26
1977:	June 21	May 7	Sept 28
	22	Sept 7	
	29		
	Aug 2		
	3		
	18		
	Sept 23		
1978:	June 26	May 9	
	Jly 31	28	
		June 29	

4.800 Lifespan

4.810 Mortality

Loss of individuals in the study site occur through emigration and mortality. A wide range of potential predators were observed in Great Wood during the study, including fox (Vulpes vulpes Linn.) badger (Meles meles Linn.), common shrew (Sorex araneus Linn.), pygmy shrew (Sorex minutus Linn.), common frog (Rana temporaria Linn.), and various birds, as well as other invertebrates such as spiders and rove beetles (Staphylinidae). The contents of a regurgitated bird pellet found near Great Wood included a whole third instar larva of Pterostichus madidus. Common and pygmy shrews were frequently found in the pitfall traps, and on many occasions broken elytra by the traps indicated their activities.

Fox droppings were collected on a number of occasions and examined for signs of carabid beetles. Summer and autumn were the best times for beetle remains, whereas they were rarely present at other times. Identifiable fragments in these faecal pellets are detailed in Table 4.22. The species composition is more like that of the adjacent fields than the wood (Table 4.23) and is probably the result of foraging expeditions and defaecation en-route to the earths within the wood.

4.820 Longevity

The results of the mark-release-recapture experiments described in the following chapters provide plenty of information on the duration of individual beetles in the study site area. The recapture of individually marked beetles is the most certain method of studying

Table 4.22: Analysis of faecal remains of fox in Great Wood

Date	Coleoptera remains	Number of commonest elytron represented
18.8.76	Most of cuticle of a <u>Carabus violaceus</u>	1
18.8.76	Numerous pieces of <u>Calathus fuscipes</u>	
20.8.76	" " " " and one <u>Pterostichus madidus</u>	29 1
13.9.76	Numerous pieces of <u>C. fuscipes</u> and one <u>Aphodius</u> sp.	
5.10.76	Elytra of one <u>P. madidus</u> and numerous pieces of <u>C. fuscipes</u>	1 10
8.10.76	Numerous pieces of <u>C. fuscipes</u> , a single <u>P. madidus</u> pair of elytra, and pieces of a <u>Geotrupes stercorarius</u> Linn.	7 1
5.5.76	None	
2.78	None	

Table 4.23: Comparison of different sources of beetle material, to demonstrate similarities between the fauna of cow pats in an adjacent field and the elytral remains within fox faeces in Great Wood

Species	June - Oct 1976 relative abundance		
	Great Wood		Meadow
	pitfalls	fox droppings	beneath cow pats
<u>P. madidus</u>	1800	3	2
<u>N. brevicollis</u>	2976	nil	nil
<u>C. fuscipes</u>	275	46	44
<u>A.parallelepipedus</u>	639	nil	nil

longevity in the field. Other methods, such as examination of the Corpora lutea in the female reproductive system (Kurka, 1972; Heerdt et al, 1976; Dijk, 1973; Gilbert, 1955), mandible wear (Houston, 1970), and the presence of mature adults before pupal eclosion (many authors), generally only indicate survival of individuals from their first season as an adult into a second. Although Houston (loc.cit) and Heerdt (loc.cit.) have both shown their methods to be sufficiently accurate to demonstrate successive years of life.

In the present study, Nebria brevicollis adults were found to have survived up to 21 months after being first captured and marked. When these individuals were considered in relation to the life history (4.200) it was seen that at least three of the beetles were active in their third breeding season (all males): first captured in March and April 1976, and recaptured in October 1977. Of the 624 beetles marked before the emergence of callow individuals in the spring of 1976, 137 (22.0%) were active in the 1976 breeding season, and, as already mentioned, three of these (2.2%) were again recorded in the 1977 breeding season. 1443 new marks were applied between September 1976 and April 1977, and of these 79 (5.4%) were recaptured in the 1977 breeding season. Thus survival into a second breeding season appears to be commonplace in this species. Whether or not mortality is affected by age cannot be commented on here as only three animals were found to have reached a third breeding season. However, the two percentages 22.0% (to second season) and 2.2% (to third season) do suggest that age does affect mortality.

With Pterostichus madidus, 1448 adults are known to have been present in the pitfall grid in the 1975 breeding season, and of these 43 (2.97%) were active in the following breeding season, 13 (30.2% of the 43) in the 1977 season, and 7 (53.8% of the 13) in 1978 - seven beetles were shown to have survived into their fourth breeding season (approximately 0.5% of the total marked in 1975). Of the marks applied from July 1976 until June 1977 (mostly the presumed new generation), 56 (4.4%) were recaptured in the 1977 breeding season, and 9 (16.1% of the 56) in the 1978 season.

The results of Abax marking are more difficult to interpret because of the extended breeding period. However, if it is assumed that mature beetles captured in April and May have overwintered from the previous year, some useful information may be generated. 148 beetles were marked in April and May 1976, and, of these, 20 (13.5%) were active in the 1976 breeding season, 7 (35% of the 20) in the 1977 season, and 5 (71.4% of the 7) in the 1978 season. So, as with Pterostichus madidus, some were clearly entering a fourth breeding season. Beetles marked from June 1976 until May 1977 numbered 367, and, of these, 19 (5.18%) were active in summer 1977, and 15 (78.9% of the 19) in summer 1978.

With Carabus violaceus, only activity in a second breeding season could be demonstrated, with only five beetles overwintering into the 1977 season (of 46 released, i.e. 10.9%), and 1 into the 1978 season (of 38 released, i.e. 2.6%). All of these were female beetles.

Pterostichus niger similarly only showed survival into a second season: 2 of the 43 marked in 1976 (4.7%), and 8 of the 256 marked in

1977 (3.1%).

Therefore, in all five species, beetles were found that entered a second breeding season. This overwintering survival was greatest in Nebria brevicollis, but this may be a reflection of the greater recapture rates seen in this species, since it is only in species with low recapture rates (Pterostichus madidus and Abax parallelepipedus) that survival into a fourth breeding season was demonstrated in a number of beetles. Carabus violaceus and Pterostichus niger captures were too low in numbers to show whether or not a similar situation exists in these species.

4.900 Summary of Chapter

Life history information derived from the mark-release-recapture studies described in Chapters 5, 6 and 7 is described for Nebria brevicollis, Pterostichus madidus, Abax parallelepipedus, Carabus violaceus and Pterostichus niger, and some preliminary comparisons with published accounts made. Supplementary information derived from dissections of adult beetles and field observations are included.

Mortality and longevity are considered, and some figures presented.

Chapter 5

The Mark-Release-Recapture programme,
1975 - 77 : A baseline study.

5.100 Introduction

The aim of this initial pitfall trapping study is to examine the dispersive behaviour of the individual carabid beetle under conditions of minimum disturbance. Results derived from procedures demonstrated earlier (Ch. 3) to alter the behaviour of the beetle are not included in the analyses.

5.200 Methods

Initially twelve pitfall traps were placed to test the suitability of the carabid populations of the woodland site, and of the marking procedure. Glass traps in the form of 1lb size jam jars were used. These were all from one brand of jam and so were of more or less constant size (mouth 53mm diameter).

During February 1976, the numbers of traps were built up, and the original 12 removed, until a 7 by 10 square-based grid of pitfall traps, positioned 15m apart, was operational from March 4 onwards. These pitfalls were at locations A - G, 1 - 10 (see Figure 2.2).

The traps were visited early each morning on five consecutive days a week, and the carabid contents transferred to clean, individually labelled, glass tubes for carriage to the laboratory. The beetles were carefully removed from the pitfalls using a pair of light forceps. In the laboratory the beetles were identified, sexed, and examined for earlier marks. Individual scratch marks were applied to the elytra of unmarked beetles (see 3.540).

For marking, the beetles were held still by apparatus shown in Figure 3.1(iii), and the marks produced by scraping the surface layers of the cuticle away with the edge of a piece of safety razor

blade at pre-determined locations on the elytra (see Figure 5.1). The whole operation being carried out under a low power binocular microscope.

The beetles were normally returned to the study site during the afternoon of the same day. On some occasions, however, the beetles were returned the following day, but, although no effects on subsequent behaviour or survival could be demonstrated (see Ch. 3.440), results following this procedure are omitted from the analysis. It seems highly probable that confinement in a small glass tube in the laboratory overnight will have a disturbing affect on the beetles.

Nebria brevicollis beetles left in the field traps over the weekend periods were found to behave differently from those released in the afternoon following capture (Ch. 3.440) and so were excluded from further analysis.

Throughout the study period trap maintenance was carried out as necessary. This included the removal of soil, litter and animals from traps, removal of water after rainfall, and keeping the mouth of the trap flush with the soil surface. The use of forceps to extract the beetles from the traps meant that the surrounding soil was rarely disturbed by the removal of the traps - an operation only necessitated by flooding with rainwater, or soil due to adjacent excavations by squirrels and rabbits.

All traps were closed, by turning the jars upside down in their pits, during the following periods:- April 14 - May 3, July 9 - 19, August 31 - September 13, 1976, March 24 - April 4, and April 13 - 25, 1977. The traps were left open but unattended for two seven day

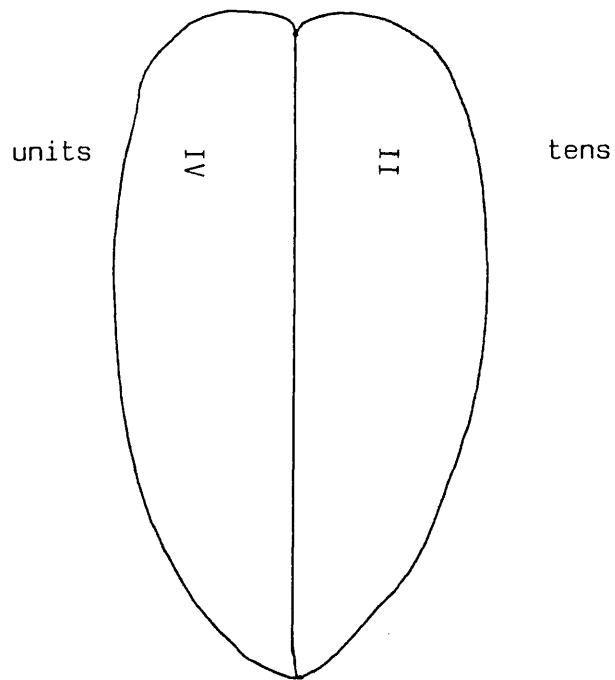
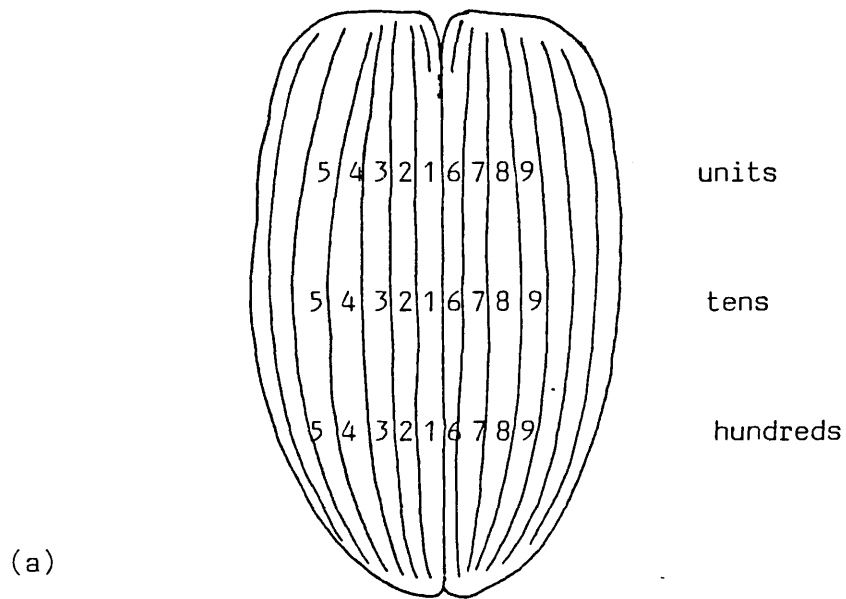


Figure 5.1 Locations on elytron used for application of individual marks.

(a) elytron with striae, (b) elytron lacking striae — Roman numerals are scratched, e.g. no. 24.

periods at the turn of the year (December - January) in both 1975/76 and 1976/77.

Throughout this trapping period marked beetles were released within one metre of the trap in which they were captured. On release they were generally observed to push their way into the leaf litter until hidden from view and then to cease movement.

In the course of this investigation pitfall traps were also in use outside the main 7 x 10 grid. From March 2 until April 12, 1976, ten plastic beakers were placed in a 2 x 5 grid at 5m intervals within the pine plantation in the corner adjoining the field and the oakwood. This grid was an experiment to compare the trapping characteristics of plastic and glass pitfalls. This grid was abandoned due to continued disturbance by mammals - the lightness of these plastic traps meant that they were easily pulled from the ground.

Larger glass jars (of 12cm diameter) were also used in the pine plantation near to the beakers, during the period March 17 - August 16, 1976. These contained cellophane baffles separating the catch into four equal chambers according to the location along the trap perimeter of the beetles on falling into the pitfall. Once again mammal disturbance led to their abandonment - the baffles were constantly removed. The use of baffles had been suggested by Mason (1972) although he never used them extensively since he found that his carabids moved in a random fashion and gave no evidence of pronounced migratory movements (Mason, 1976, personal communication).

Pitfalls were also set at locations H - K, 1 - 4 (see Figure 2.2) as part of baiting experiments described elsewhere (3.420), and were operated during April 8 - 14, May 3 - 10, May 26 - 28, August 4 - 31, 1976.

Catches derived from all of the temporary grids described above are included in the species totals (2.600) and the weekly trapping totals (Tables 5.1 - 5.5) but nowhere else.

5.300 Results and Discussion

5.310 Weekly catch totals

Weekly trapping and marking results are shown in Tables 5.1 - 5.5. It was decided to present these results in the form of weekly rather than monthly totals since the former conforms to the trapping cycle, and neither to any natural cycle. Weeks are numbered in accordance with British Standard 4760:1971.

Catches and marked releases of Pterostichus niger and Carabus violaceus are rather low but are included for comparative purposes. P. niger became more abundant in the following season.

Recapture rates for the species are brought together in Table 5.6 and the differences between the sexes tested. The difference in the rates between the sexes were only found to be significant in Abax (at the 0.1% level). Where other studies have commented on recapture rates, they have only referred to the species as a whole, not to the sexes. Comparisons are not therefore available. Generally speaking other studies also obtained low recapture rates (Drift, 1951; Greenslade, 1961; Frank, 1967b; Mason, 1972; Nield, 1974).

Table 5.1 (i): Weekly trapping totals for Nebria brevicollis adults
(continued 5.1(ii)) ("Trapping effort" is the product
of the number of traps and the number of days in operation.
Totals include beetles from traps in all grids and ex-
perimental procedures.)

Year	Month	Week No.	Catch totals		Marked-release totals		Trapping effort (traps x days)
			Unmarked	Marked	Newly marked	Old Marks	
1975	Oct/Nov	43	55	2	38	2	56
	Nov	44	24	4	21	4	35
	Nov	45	4	1	4	1	49
	Nov	46	31	1	25	1	49
	Nov	47	21	4	21	4	48
	Dec	48	55	10	45	8	87
	Dec	49	8	2	8	2	70
	Dec	50	4	1	2	1	91
	Dec	51	10	4	8	4	143
1976	Dec/Jan	52	1	3	1	2	78
	Jan	1	nil	2	-	2	52
	Jan	2	10	3	10	3	104
	Jan	3	8	4	8	4	68
	Jan	4	nil	nil	-	-	112
	Jan/Feb	5	nil	nil	-	-	98
	Feb	6	14	2	14	2	275
	Feb	7	3	1	3	1	279
	Feb	8	67	9	63	9	343
	Feb/Mar	9	18	3	18	3	334
	Mar	10	16	4	16	4	367
	Mar	11	84	14	69	14	563
	Mar	12	67	16	62	16	574
	Mar/Apr	13	78	18	73	17	576
	Apr	14	40	8	39	8	593
	Apr	15	76	15	75	15	455
	Apr/May 16 & 17		traps closed		-	-	nil
	May	18	42	3	24	3	340
	May	19	40	2	6	2	547
	May	20	8	nil	2	-	511
	May	21	23	2	8	2	527
	May/June	22	24	nil	10	-	511
	June	23	13	nil	10	-	511
	June	24	7	nil	6	-	520
	June	25	9	nil	8	-	531
	June/July	26	1	nil	1	-	532
	July	27	1	nil	1	-	532
	July	28	traps closed		-	-	nil
	July	29	nil	nil	-	-	304
	July	30	nil	nil	-	-	532
	July/Aug	31	nil	nil	-	-	568

Table 5.1 (ii) Nebria brevicollis continued

Year	Month	Week No.	Catch totals		Marked-release totals				Trapping effort		
			Unmarked	Marked	Newly marked		Old Marks				
1976	Aug	32	nil	nil	-	-	-	-	616		
	Aug	33	nil	nil	-	-	-	-	619		
	Aug	34	nil	nil	-	-	-	-	546		
	Aug/Sept	35	9	2	9		2		455		
	Sept	36	traps closed		-		-		nil		
	Sept	37	132	22	97		21		316		
	Sept	38	412	116	243		103		632		
	Sept/Oct	39	556	186	239		160		494		
	Oct	40	342	199	291		181		553		
	Oct	41	259	238	215		212		553		
	Oct	42	88	169	82		155		553		
	Oct	43	91	136	72		119		555		
	Oct/Nov	44	23	62	22		56		560		
	Nov	45	25	49	15		43		560		
	Nov	46	11	27	10		25		560		
	Nov	47	7	18	7		18		560		
	Nov/Dec	48	3	12	3		12		560		
	Dec	49	4	11	4		11		560		
	Dec	50	nil	1	-		1		480		
	Dec	51	3	1	2		-		400		
	Dec	52	4	6	4		5		640		
1977	Jan	1	4	6	3		5		240		
	Jan	2	1	2	1		1		560		
	Jan	3	1	2	1		2		560		
			♂	♀	♂	♀	♂	♀			
	Jan	4	1	3	2	1	2	2	1	560	
	Jan/Feb	5	1	nil	nil	1	-	-	1	560	
	Feb	6	2	nil	4	1	2	-	4	1	560
	Feb	7	1	nil	7	nil	1	-	6	-	560
	Feb	8	3	nil	3	nil	3	-	3	-	560
	Feb/Mar	9	3	nil	6	nil	3	-	6	-	560
	Mar	10	nil	2	3	1	-	2	3	1	560
	Mar	11	1	1	nil	1	1	-	-	1	557
	Mar	12	nil	nil	nil	nil	-	-	-	-	480
	Mar	13	traps closed		-		-		-		nil
	Apr	14	nil	1	nil	nil	-	1	-	-	320
	Apr	15	nil	nil	1	nil	-	-	1	-	320
	Apr	16	traps closed		-		-		-		nil
	Apr	17	2	nil	1	nil	1	-	1	-	320
	Apr/May	18	nil	nil	1	1	-	-	1	1	560
	May	19	7	9	3	nil	-	-	2	-	392
Totals				1440		2048		1302			

[of 3348 mark-releases 1440 recaptured i.e. 43.01%]

Table 5.2 (i): Weekly trapping totals for Pterostichus madidus adults
 (continued in 5.2(ii)) ("Trapping effort" is the product
 of the number of traps and the number of days in operation.
 Totals include beetles from traps in all grids and
 experimental procedures).

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort (traps x days)	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1975	Oct/Nov	43	nil	13	nil	nil	-	13	-	-	56	
	Nov	44	nil	6	nil	3	-	6	-	3	35	
	Nov	45	nil	2	nil	nil	-	2	-	-	49	
	Nov	46	nil	7	nil	2	-	6	-	2	49	
	Nov	47	nil	6	nil	nil	-	6	-	-	48	
	Dec	48	1	5	nil	3	1	4	-	3	87	
	Dec	49	nil	2	nil	nil	-	2	-	-	70	
	Dec	50	nil	nil	nil	nil	-	-	-	-	91	
	Dec	51	1	nil	nil	nil	1	-	-	-	143	
	Dec/Jan	52	1	nil	nil	nil	1	-	-	-	78	
1976	Jan	1	nil	nil	nil	nil	-	-	-	-	52	
	Jan	2	nil	nil	nil	nil	-	-	-	-	104	
	Jan	3	1	nil	nil	nil	1	-	-	-	68	
	Jan	4	nil	nil	nil	nil	-	-	-	-	112	
	Jan/Feb	5	nil	nil	nil	nil	-	-	-	-	98	
	Feb	6	3	2	nil	nil	3	2	-	-	275	
	Feb	7	nil	nil	nil	nil	-	-	-	-	279	
	Feb	8	13	6	1	nil	13	5	1	-	343	
	Feb/Mar	9	6	4	nil	1	5	4	-	1	334	
	Mar	10	6	1	nil	2	6	1	-	2	367	
	Mar	11	9	5	1	4	8	5	1	4	563	
	Mar	12	18	6	4	3	17	5	4	3	574	
	Mar/Apr	13	31	30	2	4	31	30	2	4	576	
	Apr	14	22	29	nil	3	22	28	-	3	593	
	Apr	15	47	38	4	9	47	33	4	9	455	
	Apr/May	16 & 17	traps closed				-	-	-	-	-	nil
	May	18	69	108	6	4	60	92	6	4	340	
	May	19	62	182	4	8	24	70	4	8	547	
	May	20	21	21	2	6	21	21	2	6	511	
	May	21	54	49	1	9	54	47	1	7	527	
	May/Jun	22	98	65	4	4	78	42	4	4	511	
	June	23	116	62	7	1	116	62	7	1	511	
	June	24	158	32	11	2	158	32	11	2	520	
	June	25	175	31	10	1	162	26	9	1	531	
	Jun/Jul	26	91	10	9	nil	87	9	9	-	532	
	July	27	43	5	4	nil	41	3	3	-	532	
	July	28	traps closed				-	-	-	-	-	nil
	July	29	57	12	3	1	51	6	3	1	304	
	July	30	119	32	17	1	112	25	17	1	532	
	July/Aug	31	77	28	10	1	72	22	10	1	568	

Table 5.2(ii): *Pterostichus madidus* (Continued).

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1976	Aug	32	81	33	8	nil	73	24	8	-	616	
	Aug	33	73	39	5	nil	71	35	4	-	619	
	Aug	34	40	12	11	3	38	12	11	3	546	
	Aug/Sep	35	95	35	13	2	50	10	10	1	455	
	Sept	36	traps closed				-	-	-	-	-	nil
	Sept	37	6	1	nil	nil	6	1	-	-	316	
	Sept	38	10	5	1	1	7	3	1	1	632	
	Sep/Oct	39	4	2	nil	nil	2	-	-	-	494	
	Oct	40	4	6	1	nil	4	5	1	-	553	
	Oct	41	11	9	3	2	9	5	3	2	553	
	Oct	42	2	15	2	1	2	11	-	1	553	
	Oct	43	3	22	1	nil	3	19	1	-	555	
	Oct/Nov	44	nil	18	2	nil	-	18	2	-	560	
	Nov	45	1	16	nil	2	1	13	-	2	560	
	Nov	46	1	19	nil	5	1	19	-	5	560	
	Nov	47	nil	5	nil	3	-	4	-	3	560	
	Nov/Dec	48	nil	6	nil	1	-	6	-	-	560	
	Dec	49	nil	2	nil	nil	-	2	-	-	560	
	Dec	50	nil	nil	nil	nil	-	-	-	-	480	
	Dec	51	nil	2	nil	nil	-	2	-	-	406	
	Dec	52	nil	1	nil	1	-	1	-	1	640	
	Jan	1	nil	nil	nil	nil	-	-	-	-	240	
	Jan	2	nil	1	nil	nil	-	1	-	-	560	
	Jan	3	nil	nil	nil	nil	-	-	-	-	560	
	Jan	4	nil	2	nil	2	-	2	-	2	560	
	Jan/Feb	5	1	nil	nil	nil	1	-	-	-	560	
	Feb	6	nil	nil	nil	nil	-	-	-	-	560	
	Feb	7	nil	nil	nil	nil	-	-	-	-	560	
	Feb	8	1	4	nil	nil	1	4	-	-	560	
	Feb/Mar	9	5	4	1	1	5	4	1	1	560	
	Mar	10	4	1	1	nil	4	1	1	-	560	
	Mar	11	nil	4	nil	1	-	4	-	1	557	
	Mar	12	nil	3	1	nil	-	2	1	-	480	
	Mar	13	traps closed				-	-	-	-	-	nil
	Apr	14	1	4	nil	nil	1	4	-	-	320	
	Apr	15	nil	3	nil	nil	-	3	-	-	320	
	Apr	16	traps closed				-	-	-	-	-	nil
	Apr	17	4	11	nil	nil	4	11	-	-	320	
	Apr/May	18	6	23	nil	2	6	22	-	2	560	
	May	19	8	26	nil	1	8	24	-	1	392	
Totals			150 100				1489	886	142	96		

[2580 beetles released marked, 250 recaptures i.e. 9.69%

♂♂ 1623 released; 150 recaptured i.e. 9.24%

♀♀ 957 released; 100 recaptured i.e. 10.45%]

Table 5.3(i): Weekly trapping totals of *Abax parallelepipedus* adults (continued in 5.3(ii)) ("Trapping effort" is the product of the number of traps and the number of days in operation. Totals include beetles from traps in all grids and experimental procedures).

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort (traps x days)	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1975	Oct/Dec	43/52	nil	nil	nil	nil	-	-	-	-	706	
1976	Jan/Mar	1/12	nil	nil	nil	nil	-	-	-	-	3169	
	Apr	13	1	1	nil	nil	1	1	-	-	576	
	Apr	14	1	1	nil	nil	-	1	-	-	593	
	Apr	15	3	9	nil	nil	3	9	-	-	455	
	Apr/May	16/17	traps closed				-	-	-	-	-	nil
	May	18	34	35	nil	1	22	23	-	1	340	
	May	19	62	44	1	3	22	13	1	3	547	
	May	20	17	6	1	nil	17	5	1	-	511	
	May	21	25	9	4	nil	23	8	4	-	527	
	May/June	22	39	22	2	nil	28	17	2	-	511	
	June	23	23	15	3	1	23	14	3	1	511	
	June	24	35	14	5	2	35	13	5	2	520	
	June	25	32	13	7	1	27	13	6	1	531	
	June/July	26	34	18	9	1	30	11	8	1	532	
	Jly	27	15	3	7	1	6	3	5	1	532	
	Jly	28	traps closed				-	-	-	-	-	nil
	Jly	29	22	12	nil	1	21	11	-	1	304	
	Jly	30	11	6	4	nil	16	6	4	-	502	
	Jly/Aug	31	3	4	5	nil	2	3	5	-	568	
	Aug	32	6	4	1	nil	5	4	1	-	616	
	Aug	33	1	1	1	nil	-	-	1	-	619	
	Aug	34	6	6	nil	nil	-	2	-	-	546	
	Aug/Sept	35	8	3	1	nil	3	3	-	-	455	
	Sept	36	traps closed				-	-	-	-	-	nil
	Sept	37	2	2	nil	nil	2	-	-	-	316	
	Sept	38	7	7	3	nil	1	2	3	-	632	
	Sept/Oct	39	8	5	nil	nil	1	3	-	-	494	
	Oct	40	5	5	nil	nil	4	3	-	-	553	
	Oct	41	3	1	nil	nil	1	1	-	-	553	
	Oct	42	2	3	nil	nil	1	3	-	-	553	
	Oct	43	1	2	nil	nil	1	1	-	-	555	
	Oct/Nov	44	nil	nil	nil	nil	-	-	-	-	560	
	Nov	45	nil	nil	nil	nil	-	-	-	-	560	
	Nov	46	nil	1	nil	nil	-	-	-	-	560	
	Nov/Dec	47/52	nil	nil	nil	nil	-	-	-	-	3206	

Table 5.3(ii): *Abax parallelepipedus* continued

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1977	Jan	1	nil	nil	nil	nil	-	-	-	-	240	
	Jan	2	nil	nil	nil	nil	-	-	-	-	560	
	Jan	3	nil	nil	nil	nil	-	-	-	-	560	
	Jan	4	nil	1	nil	nil	-	1	-	-	560	
	Jan/Feb	5	nil	nil	nil	nil	-	-	-	-	560	
	Feb	6	nil	nil	nil	nil	-	-	-	-	560	
	Feb	7	1	nil	nil	nil	1	-	-	-	560	
	Feb	8	1	nil	nil	nil	1	-	-	-	560	
	Feb/Mar	9	nil	nil	nil	nil	-	-	-	-	560	
	Mar	10	nil	nil	nil	nil	-	-	-	-	560	
	Mar	11	nil	nil	nil	nil	-	-	-	-	557	
	Mar	12	nil	1	nil	nil	-	1	-	-	480	
	Mar	13	traps closed				-	-	-	-	-	nil
	April	14	nil	nil	nil	nil	-	-	-	-	320	
	Apr	15	nil	nil	nil	nil	-	-	-	-	320	
	Apr	16	traps closed				-	-	-	-	-	nil
	Apr	17	1	1	1	nil	1	1	1	-	320	
	Apr/May	18	4	nil	1	nil	3	-	1	-	560	
	May	19	12	3	1	nil	11	2	1	-	392	
Totals					57	11	307	178	52	11		

[534 mark releases : 68 recaptures i.e. 12.73%

♂♂ 347 releases : 57 recaptures i.e. 16.43%

♀♀ 187 releases : 11 recaptures i.e. 5.88%]

Table 5.4: Weekly trapping totals for Pterostichus niger adults
 ("Trapping effort" is the product of the number of traps
 and the number of days in operation. Totals include
 beetles from traps in all grids and experimental procedures).

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1975	Oct/Dec	43/52	nil	nil	nil	nil	-	-	-	-	706	
1976	Jan/Mar	1/11	nil	nil	nil	nil	-	-	-	-	2595	
	Mar	12	1	1	nil	nil	-	-	-	-	574	
	Mar/Apr	13	nil	nil	nil	nil	-	-	-	-	576	
	Apr	14	nil	nil	1	nil	-	-	1	-	593	
	Apr	15	nil	nil	nil	nil	-	-	-	-	455	
	Apr/May	16/17	traps closed				-	-	-	-	-	nil
	May	18	2	nil	nil	nil	1	-	-	-	340	
	May	19	1	2	nil	nil	nil	nil	-	-	547	
	May	20	nil	nil	nil	nil	-	-	-	-	511	
	May	21	3	1	nil	nil	3	1	-	-	527	
	May/June	22	1	3	nil	nil	nil	3	-	-	511	
	June	23	2	2	nil	nil	2	2	-	-	511	
	June	24	nil	nil	nil	nil	-	-	-	-	520	
	June	25	2	nil	nil	nil	1	-	-	-	531	
	June/July	26	nil	1	nil	nil	-	1	-	-	532	
	July	27	2	1	nil	nil	2	1	-	-	532	
	July	28	traps closed				-	-	-	-	-	nil
	July	29	3	1	nil	1	3	1	-	1	304	
	July	30	3	2	nil	nil	3	1	-	-	502	
	July/Aug	31	1	2	nil	nil	1	2	-	-	568	
	Aug	32	2	nil	nil	nil	2	-	-	-	616	
	Aug	33	2	1	nil	nil	2	1	-	-	619	
	Aug	34	nil	1	1	nil	-	1	1	-	546	
	Aug/Sept	35	2	3	nil	nil	2	2	-	-	455	
	Sept	36	traps closed				-	-	-	-	-	nil
	Sept	37	nil	nil	nil	nil	-	-	-	-	316	
	Sept	38	1	1	1	nil	1	1	1	-	632	
	Sep/Dec	39/52	nil	nil	nil	nil	-	-	-	-	7594	
	Jan/May	1/18	nil	nil	nil	nil	-	-	-	-	7837	
	May	19	2	nil	nil	nil	2	-	-	-	392	
Totals					3	1	25	18	3	1		

[45 mark releases : 4 recaptures i.e. 8.89%

♂♂ 26 releases : 3 recaptures i.e. 11.54%

♀♀ 19 releases : 1 recapture i.e. 5.26%]

Table 5.5: Weekly trapping totals for Carabus violaceus adults

("Trapping effort" is the product of the number of traps and the number of days in operation. Totals include beetles from traps in all grids and experimental procedures).

Year	Month	Week No.	Catch totals				Marked-release totals				Trapping effort	
			Unmarked		Marked		Newly marked		Old Marks			
			♂	♀	♂	♀	♂	♀	♂	♀		
1975	Oct/Dec	43/52	nil	nil	nil	nil	-	-	-	-	706	
1976	Jan/Apr	1/18	nil	nil	nil	nil	-	-	-	-	5133	
	May	19	nil	2	nil	nil	-	nil	-	-	547	
	May	20	1	nil	nil	nil	1	-	-	-	511	
	May	21	nil	nil	nil	nil	-	-	-	-	527	
	May/June	22	nil	nil	1	nil	-	-	1	-	511	
	June	23	nil	nil	nil	nil	-	-	-	-	511	
	June	24	nil	2	nil	nil	-	2	-	-	520	
	June	25	3	4	nil	nil	1	nil	-	-	531	
	June/July	26	16	6	nil	nil	nil	2	-	-	532	
	July	27	11	18	nil	nil	3	9	-	-	532	
	July	28	traps closed				-	-	-	-	-	nil
	July	29	5	3	nil	nil	5	3	-	-	304	
	July	30	2	1	nil	2	2	1	-	2	502	
	July/Aug	31	1	1	1	nil	1	1	1	-	568	
	Aug	32	2	2	nil	nil	2	2	-	-	616	
	Aug	33	2	1	nil	nil	2	1	-	-	619	
	Aug	34	nil	nil	nil	nil	-	-	-	-	546	
	Aug/Sept	35	2	6	2	nil	2	6	2	-	455	
	Sept	36	traps closed				-	-	-	-	-	nil
	Sept	37	nil	1	nil	nil	-	1	-	-	316	
	Sept	38	nil	nil	1	nil	-	-	1	-	632	
	Sept/Dec	39/52	nil	nil	nil	nil	-	-	-	-	7594	
1977	Jan/May	1/19	nil	nil	nil	nil	-	-	-	-	8229	
Totals					5	2	19	28	5	2		

[54 mark releases : 7 recaptures i.e. 12.86%

♂♂ 24 releases : 5 recaptures i.e. 20.83%

♀♀ 30 releases : 2 recaptures i.e. 6.67%]

Table 5.6: Recapture rates (%) of the five species in first mark-release-recapture experiment. (Number of recaptures in brackets).

** Difference between the two sexes significant at the 0.1% level

Species	♂	♀	Total
<u>Nebria brevicollis</u>	-	-	43.01 (1440)
<u>Pterostichus madidus</u>	9.24 (150)	10.45 (100)	9.69 (250)
<u>Abax parallelepipedus</u>	16.43 (57)**	5.88 (11)	12.73 (68)
<u>Pterostichus niger</u>	11.54 (3)	5.26 (1)	8.89 (4)
<u>Carabus violaceus</u>	20.83 (5)	6.67 (2)	12.86 (7)

With the exception of Nield's urban studies, all of the above studies have been carried out in woodland. The Nebria rate found by Greenslade (1961) was higher than for the other species he studied, and Haines (1973) obtained useful rates from Nebria and Abax. Thus, although the recapture rate of Nebria in this study appears to be exceptional, the other species' rates appear to be fairly typical.

5.320 The Spatial Distribution of the Species

The catch totals for each of the five species in the 7 x 10 grid of pitfalls are displayed in figures 5.2 - 5.3. For each, the mean catch per trap location and its variance has been calculated and compared in the form of an index of dispersion (s^2/\bar{x} , after Southwood, 1966). All five calculated indices were found to be aggregated and were significantly different from a Poisson Distribution (Table 5.7). This index does not take into account aggregation of the locations, only of the beetles in each location. Southwood (loc.cit.) points out that with contagious populations the value of the index varies with the size of the sample. This effect can clearly be seen from Table 4.6, where the commonest species have the highest indices. The value for Nebria stands out from the rest and must reflect a highly contagious distribution in this species.

It cannot be assumed that the region between two traps producing high catches would also produce high catches if sampled. The inter-trap distances in this study are large at 15m and habitat changes are likely over such distances. Thus aggregation of "good" and "bad" traps is not really a useful aspect to consider in detail. However, visual examination of the distributions does indicate a high degree of aggregation (Fig. 5.3).

Figure 5.2(i): Spatial distribution of Nebria brevicollis

(\bar{x} 52.19, s^2 2515.02: s^2/\bar{x} 48.19)

	A	B	C	D	E	F	G	Total
10	13	27	14	51	20	19	20	164
9	16	54	5	7	44	49	52	227
8	9	50	21	13	28	117	35	273
7	253	68	77	61	101	93	80	733
6	28	63	160	101	135	93	120	700
5	58	11	27	3	38	4	63	204
4	23	61	86	160	186	102	103	721
3	10	1	62	40	62	92	-	267
2	5	11	33	2	57	15	45	168
1	23	16	2	6	129	6	14	196
Total	438	362	487	444	800	590	532	3653

Figure 5.2(ii): Spatial distribution of Pterostichus madidus

(\bar{x} 38.81, s^2 376.36: s^2/\bar{x} 9.70)

	A	B	C	D	E	F	G	Total
	19	49	33	31	16	26	7	181
	25	35	37	20	24	20	41	202
	42	39	21	55	17	26	19	219
	54	54	41	32	17	40	38	276
	37	51	74	70	68	69	93	459
	46	33	29	13	42	30	49	242
	40	44	37	69	21	75	59	345
	35	46	30	51	41	61	41	305
	24	22	17	13	44	62	102	284
	4	26	41	37	30	51	15	204
Total	326	399	360	391	320	460	461	2717

Figure 5.2 (iii): Spatial distribution of Abax parallelepipedus

(\bar{x} 9.63, s^2 33.52 : s^2/\bar{x} 3.48)

	A	B	C	D	E	F	G	Total
10	6	11	17	15	21	22	9	101
9	7	19	16	10	8	10	2	72
8	12	10	6	10	5	3	7	53
7	6	5	2	5	1	8	18	45
6	2	9	6	16	8	16	6	63
5	6	15	22	19	17	13	15	107
4	9	12	12	14	4	5	9	65
3	17	6	5	5	19	13	7	72
2	21	8	5	3	8	9	17	71
1	2	7	2	4	2	3	5	25
Total	88	102	93	101	93	102	95	674

Figure 5.2 (iv): Spatial distribution of Carabus violaceus

(\bar{x} 1.43, s^2 4.88 : s^2/\bar{x} 3.42)

	A	B	C	D	E	F	G	Total
8	3	-	-	-	1	1	-	8
2	-	-	1	-	-	1	-	2
6	1	1	1	2	1	-	-	6
1	-	-	1	-	-	-	-	1
10	1	4	1	3	1	-	-	10
26	-	12	3	7	3	1	-	26
11	4	2	-	-	-	3	2	11
13	2	2	1	1	3	2	2	13
23	-	2	-	8	1	4	8	23
-	-	-	-	-	-	-	-	-
Total	11	26	8	21	10	12	12	100

Figure 5.2 (v): Spatial distribution of Pterostichus niger
 (\bar{x} 0.74, s^2 1.49 : s^2/\bar{x} 2.01)

	A	B	C	D	E	F	G	Total
10	-	-	-	-	1	1	1	3
9	1	1	-	1	1	3	1	8
8	1	-	-	7	1	-	1	10
7	-	2	2	-	1	-	-	5
6	-	-	-	1	2	1	-	4
5	-	-	-	-	1	-	-	1
4	-	3	-	1	-	1	1	6
3	2	1	1	-	5	2	-	11
2	-	-	-	1	-	3	-	4
1	-	-	-	-	-	-	-	-
Total	4	7	3	11	12	11	4	52

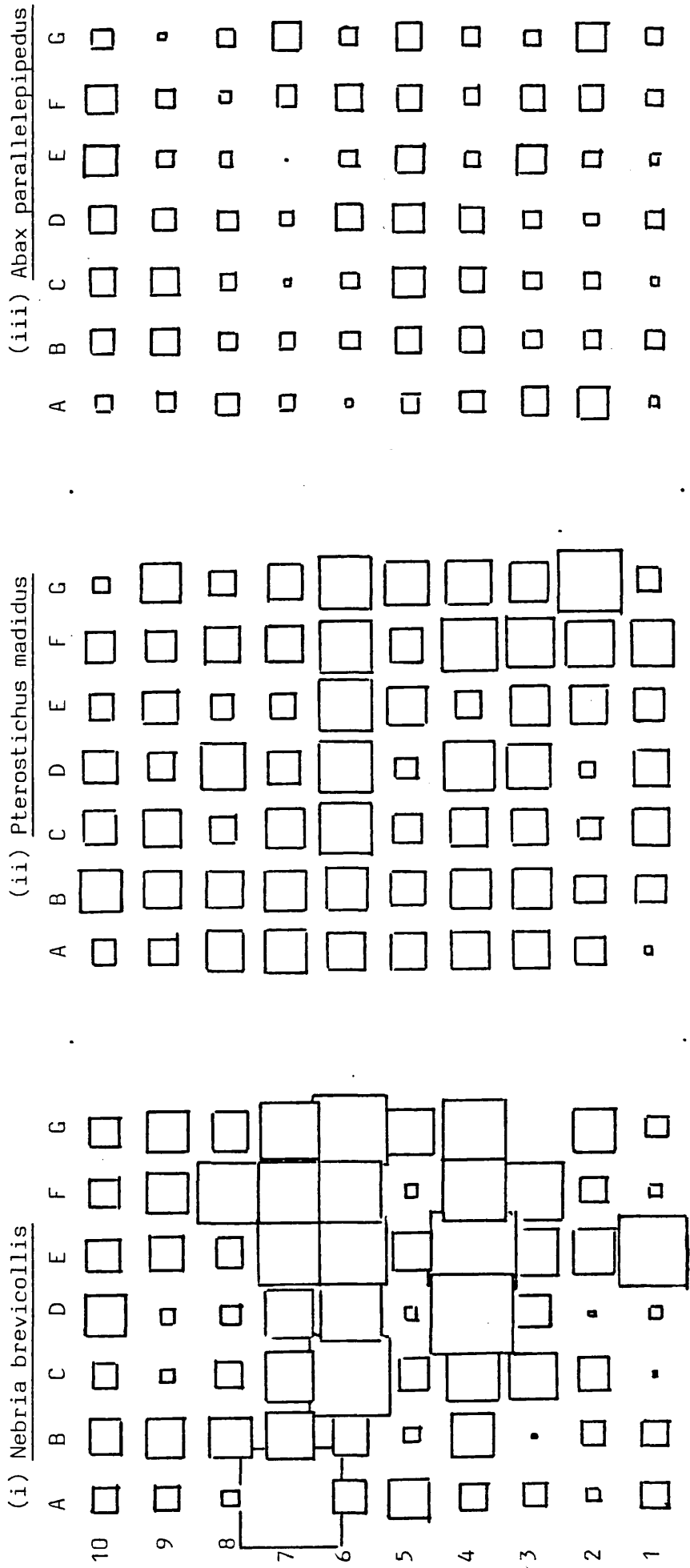


Figure 5.3 Graphical representation of the beetles' spatial distribution.
 (Volume of square represents size of catch per location : 1mm² ≡ 1 beetle).

(iv) Carabus violaceus

(v) Pterostichus niger

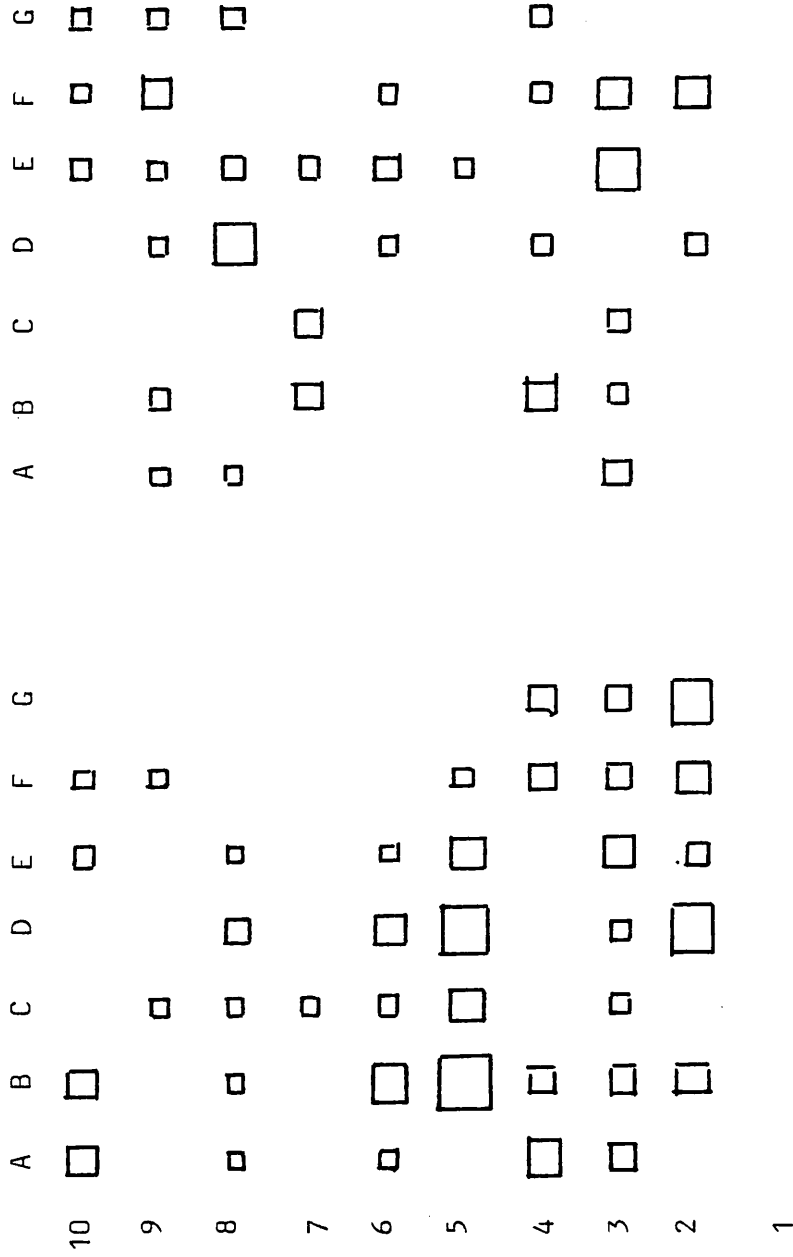


Figure 5.3 continued
 [(iv) + (v) Scale increased x 4]

Table 5.7: Comparison of dispersion characteristics for the species.
 (with 70 traps, all are significantly different from a
 Poisson distribution).

Species	Total No. of beetles	Catch per trap (\bar{x})	Variance (s^2)	s^2/\bar{x} Index of Dispersion
<u>Nebria brevicollis</u>	3653	52.19	2515.02	48.19
<u>Pterostichus madidus</u>	2717	38.81	376.36	9.70
<u>Abax parallelepipedus</u>	674	9.63	33.52	3.48
<u>Carabus violaceus</u>	100	1.43	4.88	3.42
<u>Pterostichus niger</u>	52	0.74	1.49	2.01

Aggregated distributions are well known in the Carabidae (e.g. Greenslade, 1964c; Haines, 1973; Thiele, 1977), particularly in Nebria brevicollis (Drift, 1951; Greenslade, 1964c). There are two, alternative, explanations: (i) there is an active attraction of the beetles to other beetles, or (ii) the attraction is to certain habitat characteristics and so results from patchiness of habitat. This question has already been discussed (3.420) and it is sufficient here to say only that the latter appears to be the correct explanation.

The possibility of changes in dispersion with season was also considered. This is best investigated in Nebria brevicollis where there are two peaks in adult numbers (see 4.200), the first, spring, peak is the result of feeding activity of overwintered adults, and later of newly emerged adults, and the second, autumn peak of reproductively mature adults seeking mates or oviposition sites, in addition to feeding. The catch totals of each location during the periods March - June and August - October, 1976 (Figure 5.4) were compared by calculating Spearman's Rank Correlation Coefficient, r_s . This is a distribution-free test of the degree of correlation between two sets of ranks. The value for " r_s " obtained was 0.516, and this converted to a value of Student's "t" was found to be a significant positive correlation ($t = 4.97$, with 68 degrees of freedom : $P < 0.001$ for no correlation). Thus no difference was demonstrated between the dispersion of Nebria beetles in the study site in spring and autumn 1976. Feeding activity then involves the same areas of the site as does breeding activity.

The four other species being investigated do not show two activity peaks each year and, therefore, do not readily lend themselves to the

	A	B	C	D	E	F	G	A	B	C	D	E	F	G
10	-	-	-	-	2	1	5	13	27	14	48	18	18	14
9	1	1	1	-	-	-	11	14	51	4	5	41	48	41
8	4	4	-	-	5	7	5	5	42	21	12	20	74	24
7	20	10	8	8	11	8	21	215	58	65	50	74	81	60
6	12	11	19	15	25	47	56	15	48	104	84	75	38	56
5	5	1	10	3	5	1	9	50	10	15	-	34	3	41
4	2	1	4	8	24	7	1	21	59	61	146	144	88	97
3	1	-	1	1	-	1	-	9	1	51	39	52	70	-
2	4	4	5	2	5	-	22	1	6	27	-	48	15	22
1	8	3	-	1	5	-	-	6	2	1	5	102	5	13

(i) March - June 1976
Catch totals

(ii) August - October 1976
Catch totals

	A	B	C	D	E	F	G	A	B	C	D	E	F	G
10	$8\frac{1}{2}$	$8\frac{1}{2}$	$8\frac{1}{2}$	$8\frac{1}{2}$	31	23	$43\frac{1}{2}$	$19\frac{1}{2}$	$34\frac{1}{2}$	22	$44\frac{1}{2}$	$27\frac{1}{2}$	$27\frac{1}{2}$	22
9	23	23	23	$8\frac{1}{2}$	$8\frac{1}{2}$	$8\frac{1}{2}$	59	22	$49\frac{1}{2}$	9	$11\frac{1}{2}$	40	$44\frac{1}{2}$	40
8	37	37	$8\frac{1}{2}$	$8\frac{1}{2}$	$43\frac{1}{2}$	$48\frac{1}{2}$	$43\frac{1}{2}$	$11\frac{1}{2}$	42	$30\frac{1}{2}$	18	29	$59\frac{1}{2}$	33
7	64	$56\frac{1}{2}$	52	52	59	52	65	70	53	57	$47\frac{1}{2}$	$59\frac{1}{2}$	62	55
6	61	59	63	62	68	69	70	25	$44\frac{1}{2}$	67	63	61	37	52
5	$43\frac{1}{2}$	23	$56\frac{1}{2}$	$33\frac{1}{2}$	$43\frac{1}{2}$	23	55	$47\frac{1}{2}$	17	25	2	36	8	40
4	31	23	37	52	67	$48\frac{1}{2}$	23	$30\frac{1}{2}$	54	56	69	68	64	65
3	23	$8\frac{1}{2}$	23	23	$8\frac{1}{2}$	23	$8\frac{1}{2}$	16	5	$49\frac{1}{2}$	38	51	58	2
2	37	37	$43\frac{1}{2}$	31	$43\frac{1}{2}$	$8\frac{1}{2}$	66	5	$14\frac{1}{2}$	$34\frac{1}{2}$	2	$44\frac{1}{2}$	25	32
1	52	$33\frac{1}{2}$	$8\frac{1}{2}$	23	$43\frac{1}{2}$	$8\frac{1}{2}$	$8\frac{1}{2}$	$14\frac{1}{2}$	7	5	$11\frac{1}{2}$	66	$11\frac{1}{2}$	$19\frac{1}{2}$

(iii) March - June 1976
Ranked totals

(iv) August - October 1976
Ranked totals

Figure 5.4: *Nebria brevicollis* : catch totals in spring and autumn 1976, as such, and ranked for calculation of Spearman's " r_s ".

$$[\Sigma d^2 = 28269.25, D = 28948.25 \therefore r_s = +0.516]$$

above type of analysis. However, with Pterostichus madidus, it is known that oviposition begins at the end of July and continues into the autumn (4.300). Therefore a comparison was made between the dispersion of captures early in the season (May - July) and those taken later, when oviposition is presumed to be proceeding (August - October, 1976).

Grüm (1962) studied the horizontal distribution of larvae and adults of a number of species and found that high larval catches correspond with low adult catches, and vice versa. He concluded that females leave their normal foraging grounds to seek oviposition sites elsewhere. With this in mind, only the female P. madidus beetles were examined. Spearman's " r_s " was found to be 0.24 (Figure 5.5), but the level of significance was only marginal ($t = 2.01$ with 68 degrees of freedom : $P \approx 0.05$ for no correlation).

The life history of Abax parallelepipedus (4.400) makes this kind of analysis impossible, and too few captures were made of the other two species.

5.330 Variation in catch size per trap location

The degree of aggregation found in the populations of the five species has already been well demonstrated (5.320). However, another approach can be made to analysing the cause or causes. The frequency distributions of the daily catch per trap are shown in Tables 5.8 - 5.11. As Southwood (1966) notes, at low densities the probability of any individual being found at any one location becomes indistinguishable from randomness. At higher densities the distributions became clearly contagious, as illustrated with the Nebria results (Table 5.8).

	A	B	C	D	E	F	G	A	B	C	D	E	F	G
10	4	5	5	5	5	3	-	2	2	-	1	2	1	-
9	1	5	5	9	5	2	5	5	6	1	-	1	2	4
8	6	6	1	9	4	8	3	4	3	3	2	1	1	1
7	12	6	5	7	3	8	10	5	3	5	2	1	1	1
6	9	8	17	5	23	34	32	1	3	2	8	2	1	3
5	11	8	9	3	5	9	9	2	-	1	-	3	2	5
4	8	11	8	18	6	10	8	4	2	1	3	5	7	6
3	4	4	6	8	5	8	11	2	-	4	2	3	2	-
2	4	3	1	2	10	9	20	-	4	2	-	3	11	6
1	1	9	20	10	14	14	1	-	-	4	1	3	7	1

(i) March - July 1976
Catch totals

(ii) August - October 1976
Catch totals

	A	B	C	D	E	F	G	A	B	C	D	E	F	G
10	16	24½	24½	24½	24½	11	1	35	35	6	19½	35	19½	6
9	4	24½	24½	49½	24½	7½	24½	61	65	19½	6	19½	35	55½
8	33	33	4	49½	16	41	11	55½	47½	47½	35	19½	19½	19½
7	61	33	24½	36	11	41	55½	61	47½	61	35	19½	19½	19½
6	49½	40	64	24½	68	70	69	19½	47½	35	69	35	19½	47½
5	59	40	49½	11	24½	49½	49½	35	6	19½	6	47½	35	61
4	41	59	41	65	33	55½	41	55½	35	19½	47½	61	67½	65
3	16	16	33	41	24½	41	59	35	6	55½	35	47½	35	6
2	16	11	4	7½	55½	49½	66½	6	55½	35	6	47½	70	65
1	4	49½	66½	55½	62½	62½	4	6	6	55½	19½	47½	67½	19½

(iii) March - July 1976
Ranked totals

(iv) August - October 1976
Ranked totals

Figure 5.5: Pterostichus madidus: (females): catch totals before and during oviposition period, as such, and ranked for calculation of Spearman's "r_s".

[$\Sigma d^2 = 42491.5$, $D = 43629.17$ $\therefore r_s = +0.237$]

Table 5.8: Nebria brevicollis: frequency distribution of daily catch per trap - each tested against Poisson Distribution * = $P < 0.001$

	Catch per trap																		Trap Days	No. of beetles	Beetles per trap per-day (\bar{x})	Variance of \bar{x} (s^2)	Ratio s^2/\bar{x}	Poisson probability															
	nil	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17							18														
1976	nil	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18																				
March	880	63	20	13	2		1	1												980	167	0.170	0.403	2.365	*														
April	497	44	9	7	1		1	1												560	102	0.182	0.453	2.489	*														
May	1083	30	7																	1120	44	0.039	0.050	1.280	*														
June	1103	17																		1120	17	0.015	0.015	0.985	*														
July	980																			980	nil	nil	nil	1.000															
August	1117	2	1																	1120	4	0.004	0.005	1.486															
Sept	521	131	68	38	39	14	8	9	2	4	1	1	1	1	1				840	840	1.000	3.665	3.665	*															
Oct	771	207	94	49	26	16	12	6	6			2							1190	928	0.780	2.348	3.011	*															
Nov	779	44	10	4	2	1													840	89	0.106	0.200	1.884	*															
Dec	830	5	2	3															840	18	0.021	0.047	2.206	not tested															
1977																																							
Jan	966	14																		980	14	0.014	0.014	0.986	not tested														
Feb	964	15	1																	980	17	0.017	0.019	1.105	not tested														
March	1038	12																		1050	12	0.011	0.011	0.991	not tested														
April	557	3																		560	3	0.005	0.005	0.989	not tested														
May	408	10	1	1																420	15	0.036	0.054	1.501	not tested														
Totals	12494	597	213	115	68	33	20	17	10	4	1	3	1	1	1	1	1	1	1	13580	2270	0.167	0.598	3.575															

Table 5.9: Pterostichus madidus (females): frequency distribution of daily catch per trap.

	Catch per trap					Trap Days	No. of Beetles	Beetles per trap (\bar{x})	Variance of \bar{x} (s^2)	Ratio s^2/\bar{x}
	nil	1	2	3	4					
1976 Mar	955	25				980	25	0.026	0.025	0.975
Apr	504	52	2	2		560	62	0.111	0.127	1.149
May	993	104	15	6	2	1120	160	0.143	0.203	1.421
June	1008	94	8			1120	110	0.098	0.103	1.048
July	946	33	1			980	35	0.036	0.036	1.021
Aug	1062	53	4	1		1120	64	0.057	0.067	1.162
Sept	833	7				840	7	0.008	0.008	0.991
Oct	1156	33	1			1190	35	0.029	0.030	1.028
Nov	808	30	2			840	34	0.040	0.044	1.078
Dec	837	3				840	3	0.004	0.004	0.998
1977 Jan	979		1			980	2	0.002	0.004	2.0
Feb	976	4				980	4	0.004	0.004	0.999
Mar	1040	10				1050	10	0.009	0.009	0.991
Apr	549	12	1			560	14	0.025	0.028	1.119
May	397	20	3			420	26	0.062	0.073	1.164
Totals	13051	480	38	9	2	13580	591	0.044	0.053	1.217

Table 5.10: Pterostichus madidus (males): frequency distribution of daily catch per trap

	Catch per trap							Trap Days	No. of Beetles	Beetles per trap per day (\bar{x})	Variance of \bar{x} (s^2)	Ratio s^2/\bar{x}
	1	2	3	4	5	6	7					
	nil											
1976	935	42	3					980	48	0.049	0.053	1.077
Apr	521	37	2					560	41	0.073	0.075	1.026
May	1027	80	8	2				1120	113	0.101	0.143	1.414
June	846	204	51	14	4		1	1120	371	0.331	0.468	1.414
July	839	113	27	1				980	170	0.173	0.205	1.182
Aug	965	135	19	1				1120	176	0.157	0.172	1.094
Sept	831	8	1					840	10	0.012		
Oct	1180	10						1190	10	0.008		
Nov	838	2						840	2	0.002		
Dec	840							840	nil	nil		
1977	980							980	nil	nil		
Jan	979	1						980	1	0.001		
Feb	1040	10						1050	10	0.009		
Mar	555	5						560	5	0.009		
Apr	411	8	1					420	10	0.024		
May												
Totals	12787	655	112	19	6		1	13580	967	0.071	0.100	1.396

Table 5.11: Abax parallelepipedus, Carabus violaceus, Pterostichus niger frequency distributions of daily catch per trap. [Number of trap days as in Tables 5.8, 5.9 and 5.10; number of nil captures not shown]

	Catch per trap													
	<u>Abax parallelepipedus</u>			<u>Carabus violaceus</u>			<u>Pterostichus niger</u>							
	δ	φ		δ	φ		δ	φ						
	1	2	3	1	2	3	1	2	3	1				
1976														
March	4			5							1			
April	55	3		35	2	1								
May	84	6		39	2									
June	34	4		16	1		1	7			4			
July	14			8			15	2	1		3			
Aug	12	1		7	1		4				3			
Sept	5	1		3			1				1			
Oct														
Nov														
Dec														
1977														
Jan				1										
Feb	2													
March				1										
April	1			1										
May	12			3							1			
Totals	223	15		120	6	1	28	1	1	27	2	1	20	12

Where this approach to the analysis of the trapping results differs from those used in Ch. 5.320 is that it shows that the distribution of catches per trap is unimodal. If locations within the study site were either "good" or "bad" for the beetles, then a bimodal distribution would be expected : there would be many large catches and many small catches, but few in between. This clearly is not so - there is a wide spectrum of "attractiveness" of the site locations.

5.340 Frequency of recapture of the marked beetles

The distributions of the recapture frequencies of the individual beetles are shown in Table 5.12. If each capture is independent of any previous captures, then the frequency distribution should be comparable with the Poisson Distribution. This was found to be the case for each sex of the species with the exceptions of Nebria brevicollis, where the sexes were not separated, and females of Pterostichus madidus. In both these cases too many multiple recaptures were found. The significance is real, and not a product of different sample sizes, since P. madidus and Abax parallelepipedus males both were large samples but were not significantly different from a Poisson Distribution.

There are three possible explanations for the presence of many multiple recaptures : the beetles exhibit (i) trap-proneness, or "trap-happiness", or (ii) site attachment, or (iii) the foraging technique makes them more susceptible to capture. In (i) and (ii), the beetles are either attracted to the traps themselves, or to the location of the traps, respectively. The former idea seems unlikely since it has been shown elsewhere (3.420) that the presence of other

Table 5.12: Recapture frequencies of the beetles : all recaptures Oct 1975 - May 11, 1977.

Species	Sex	No. released marked	Captured once	Recaptured								Total Recaptures (Individuals)	Poisson Distribution Probability	χ^2	
				x1	2	3	4	5	6	7	8				
<u>Nebria brevicollis</u>	♂ ♀	2048	1211	484	206	84	39	15	6	2	1	1437	(837)	P<0.001	** 459.5
<u>Pterostichus madidus</u>	♂	1488	1348	131	7	2						151	(140)	0.70>P>0.50	2.098
	♀	885	801	70	13	1						99	(84)	P<0.001	** 17.73
<u>Abax parallelepipedus</u>	♂	307	259	40	7	1						57	(48)	0.20>P>0.10	5.018
	♀	178	167	11								11	(11)	0.98>P>0.95	0.008
<u>Pterostichus niger</u>	♂	25	22	3								3	(3)	0.95>P>0.90	0.013
	♀	18	17	1								1	(1)	0.98>P>0.95	0.001
<u>Carabus violaceus</u>	♂	19	16	2		1						5	(3)	0.70>P>0.50	1.382
	♀	28	26	2								2	(2)	0.98>P>0.95	0.003

beetles is not a source of attraction, and the chances of finding food inside the traps depends on the activity of the prey animals, and is not therefore reliable.

The second idea, site attachment, cannot be concentrated on here as the analysis does not separate multiple recaptures in single traps from multiple traps, but will be returned to later (Chapter 6).

The third explanation of the multiple recaptures being resultant from foraging techniques seems the most likely for Nebria brevicollis since this species is a very active predator (4.200), and, travelling relatively quickly, may be more trappable by pitfalls.

5.350 Dispersive Behaviour of the Marked Beetles (March 4, 1976 - May 11, 1977)

5.351 Basis for analysis

Recaptured beetles are taken as sample observations at discrete points in time. An assumption basic to this study is that captured beetles are a representative sample of the whole population of the species - marked beetles are assumed to behave in the same way as unmarked ones. This has been tested to some extent in Chapter 3 with no contradictory results.

A recaptured beetle provides the following information:

- (i) the beetle has moved distance 'd' within the time interval 't', but the duration and rates of movements are unknown,
- (ii) the distance achieved (d) is the nett displacement by time 't', but the actual distance walked by the beetle is unknown, but greater than 'd',
- (iii) the individual beetle has persisted within the study by time 't'; that is, no mortality or emigration, or else emigration plus

return.

All recaptures are the result of a nett displacement since release points vary from 1 metre upwards from the traps.

It is assumed that the events of a previous capture are not remembered by the individuals at a following capture. This assumption was tested using Nebria brevicollis results from the second activity peak (Table 5.13), and found to be acceptable in this case (χ^2 value of 4.09, with five degrees of freedom : $0.7 > P > 0.5$).

The time intervals between captures of individual beetles give information on activity at the individual level, and nett displacements give information on the dispersal levels.

The duration and rates of movement are likely to change with season, so, for the purposes of this analysis, only recaptures with intervals of 30 days and less between successive captures are considered. This puts some control on the time factor and allows consideration of the nett displacements observed.

A grid of traps naturally limits the distances at which the beetle may be captured : once a beetle leaves the grid, it cannot be recaptured unless it returns. Thus large time intervals cannot result in large displacements, and so displacement rates with large inter-capture intervals will be misleading.

Where an individual can be shown to have overwintered (1975/76) and become active again in the new year it is considered separately. Thus the second age category will contain some overwintered beetles but, hopefully, the majority will be from the new generation which

Table 5.13: Nebria brevicollis recapture results for the autumn activity period 1976

(i) displayed according to the number of previous captures

(ii) results totalled for analysis as a 2 x 6 contingency table

($\chi^2 = 4.0916$, with 5 degrees of freedom : $0.7 > P > 0.5$)

(i)

		Overwintered beetles			New generation beetles		
1976	Week	Displacement by recapture no:			Displacement by recapture no:-		
	No.	1	2	3 +	1	2	3 +
		1m \geq 15m	1m \geq 15m	1m \geq 15m	1m \geq 15m	1m \geq 15m	1m \geq 15m
Sept	37	0 0	3 1	0 1	22 11	5 0	0 1
Sept	38	0 2	3 2	1 3	16 23	7 4	1 1
Oct	39	0 0	1 3	1 0	22 38	4 9	3 5
Oct	40	0 0	0 1	1 0	7 19	4 5	5 7
Oct	41	0 0	0 0	0 0	5 9	8 7	6 1
Totals		0 2	7 7	3 4	72 100	28 25	15 15

(ii)

Displacements	Overwintered beetles			New Generation			Grand Total
	1st	2nd	3 +	1st	2nd	3 +	
1m	0	7	3	72	28	15	125
\geq 15m	2	7	4	100	25	15	153
Total	2	14	7	172	53	30	278

has emerged early in the summer.

Statistics based on the recapture results are only useful for comparative purposes since the characteristics of the square-based grid of traps will introduce biases.

Distances achieved by the marked beetles on recapture are adjusted to the nearest whole metre since they are calculated on the basis of the square-based grid of traps. The character of the woodland floor surfaces means accuracy here is fallacious.

5.352 Nebria brevicollis

The recapture results for this species can be found in Appendix 5.1. The individual results have been grouped according to displacement distance with time (Fig. 5.6), intervals between captures with season (Fig. 5.7) and change in displacement with season (Fig. 5.8). These results are further analysed in tables 5.14 - 5.16 respectively.

Unfortunately too few beetles known to have overwintered were trapped for the results to be analysed in detail. However, a visual appraisal of the information in figure 5.6 (i) and (ii) shows that few large displacements occurred in the spring period, whereas many are seen in the autumn. The frequency of large displacements in the autumn is comparable with the results obtained for the beetles not known to have overwintered from the previous year. The results from this latter group of beetles will now be examined.

The mean displacement of individual beetles at one day after release is 8.92m, and 21.47m after 2-3 days (Table 5.14). The sudden jump here is probably an artefact due to the problem of some beetles

Displacement (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
67																															
64																															
62																															
60																															
54																															
47																															
45																															
42						1																									
34																															
30																															
21												1		1	1																
15							1																								
0					1		1																								

Interval (Days) between successive captures

Fig. 5.6(i) Nebria brevicollis : Displacement rate within 30 days of release.
 Beetles known to have overwintered; March - May 1976.

Displacement (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
105																														
101																														
96																														
95																														
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Intervals (Days) between successive captures

Figure 5.6(iii): *Nebria brevicollis* : Displacement rate within 30 days of release
 Beetles with no evidence for overwintering; September - November 1976.

Table 5.14: Nebria brevicollis: Analysis of displacements with time during 30 day period (figures taken from Figure 5.6(iii)).

Days between successive captures	Number of recaptures	Sum of displacements (m)	Mean displacement (m)	Variance of mean	Standard error
1	102	910	8.92	273.26	1.64
2-3	38	816	21.47	450.58	3.44
4-5	33	759	23.00	581.44	4.20
6-7	33	1246	37.76	767.09	4.82
8-9	33	914	27.70	432.47	3.62
10-13	35	1063	30.37	577.24	4.06
14-18	30	1040	34.67	535.26	4.22
19-30	27	879	32.56	361.00	3.65

Intervals (days) between successive recaptures	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30							
10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1							
11																																					
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Fig. 5.7(i) *Nebria brevicollis*: Beetles known to have overwintered - change in recapture interval with season.

(Spring 1976) Date of recapture (Week Numbers) (Spring 1977)

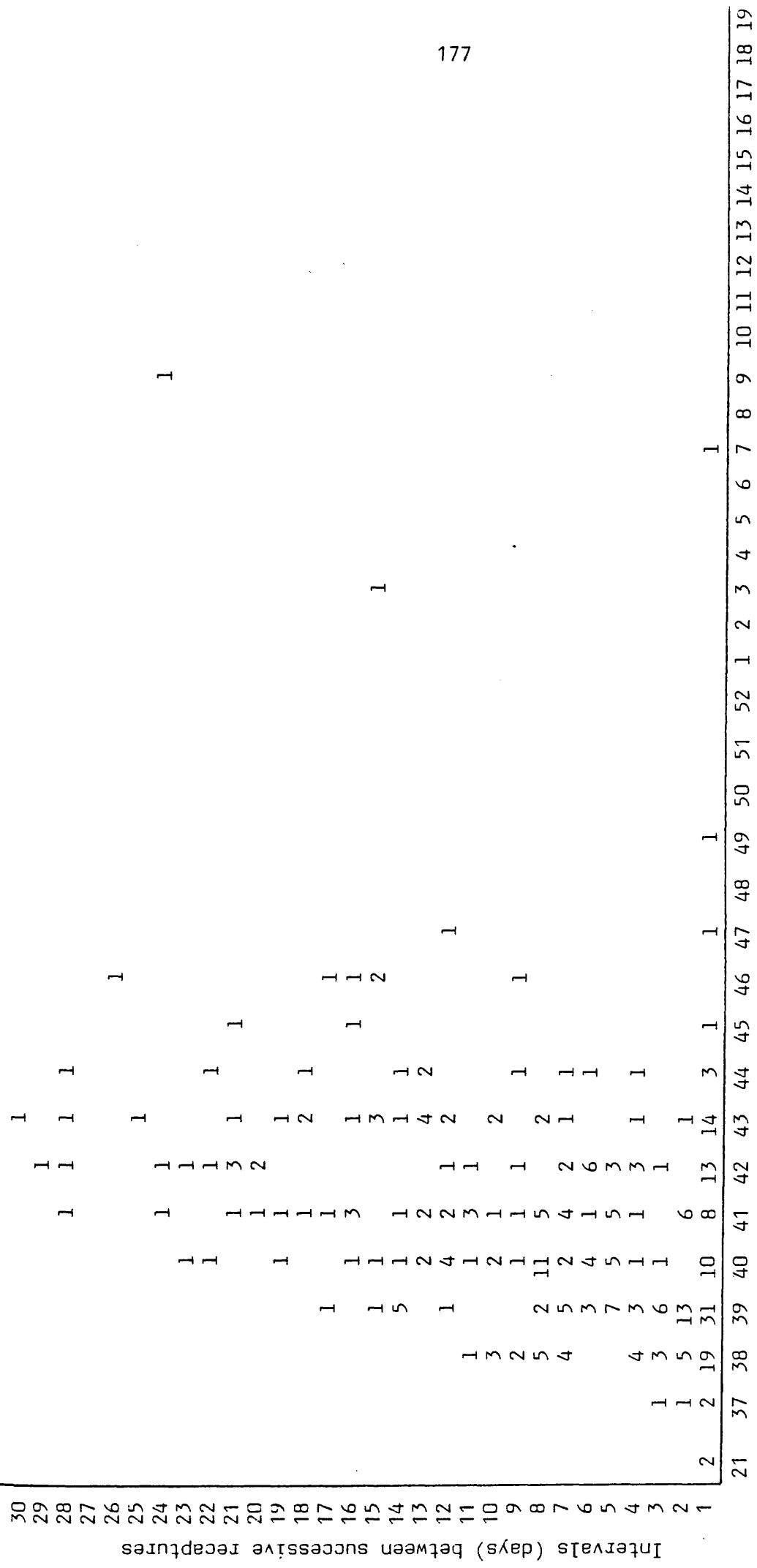


Fig. 5.7(ii) Nebria brevicollis: Beetles not known to have overwintered 1975/76. Date of recapture (week nos.) 976-77).

Table 5.15: Nebria brevicollis: Analysis of intervals between captures, within 30 day periods. (Figures from Figure 5.7 (ii))

Year	Month	Week Nos.	Number of recaptures	Sum of intervals (days)	Mean interval (days)	Variance of mean	Standard error
1976	Sept	37-38	50	188	3.76	10.96	0.47
		39	78	305	3.91	16.71	0.46
		40	50	391	7.82	28.89	0.76
	Oct	41	50	434	8.68	46.26	0.96
		42	41	354	8.63	77.14	1.37
		43	38	352	9.28	69.17	1.35
	Nov	44-49	26	308	11.85	67.97	1.62

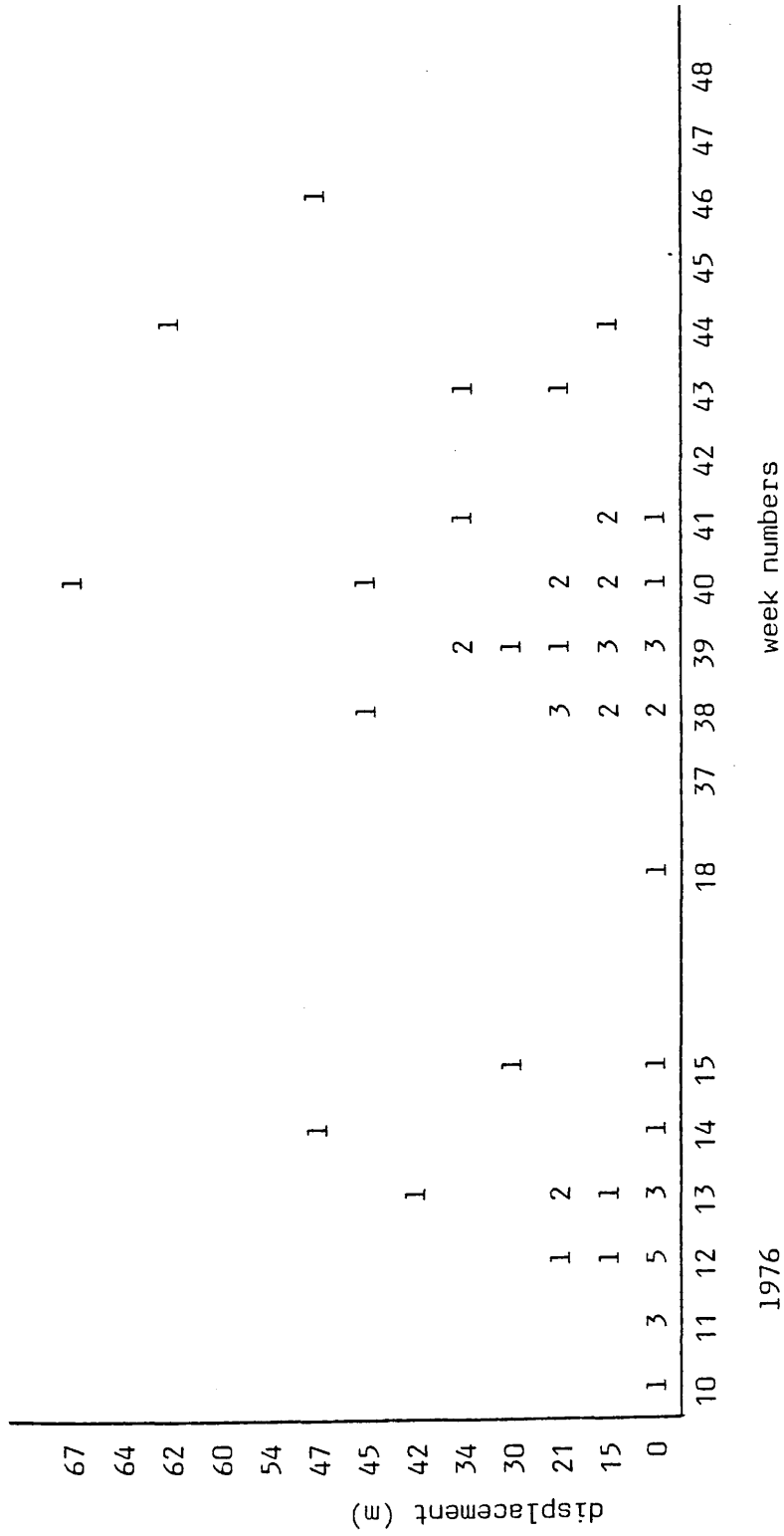


Fig 5.8 Nebria brevicollis (i) overwintered beetles.
Change in displacement with season

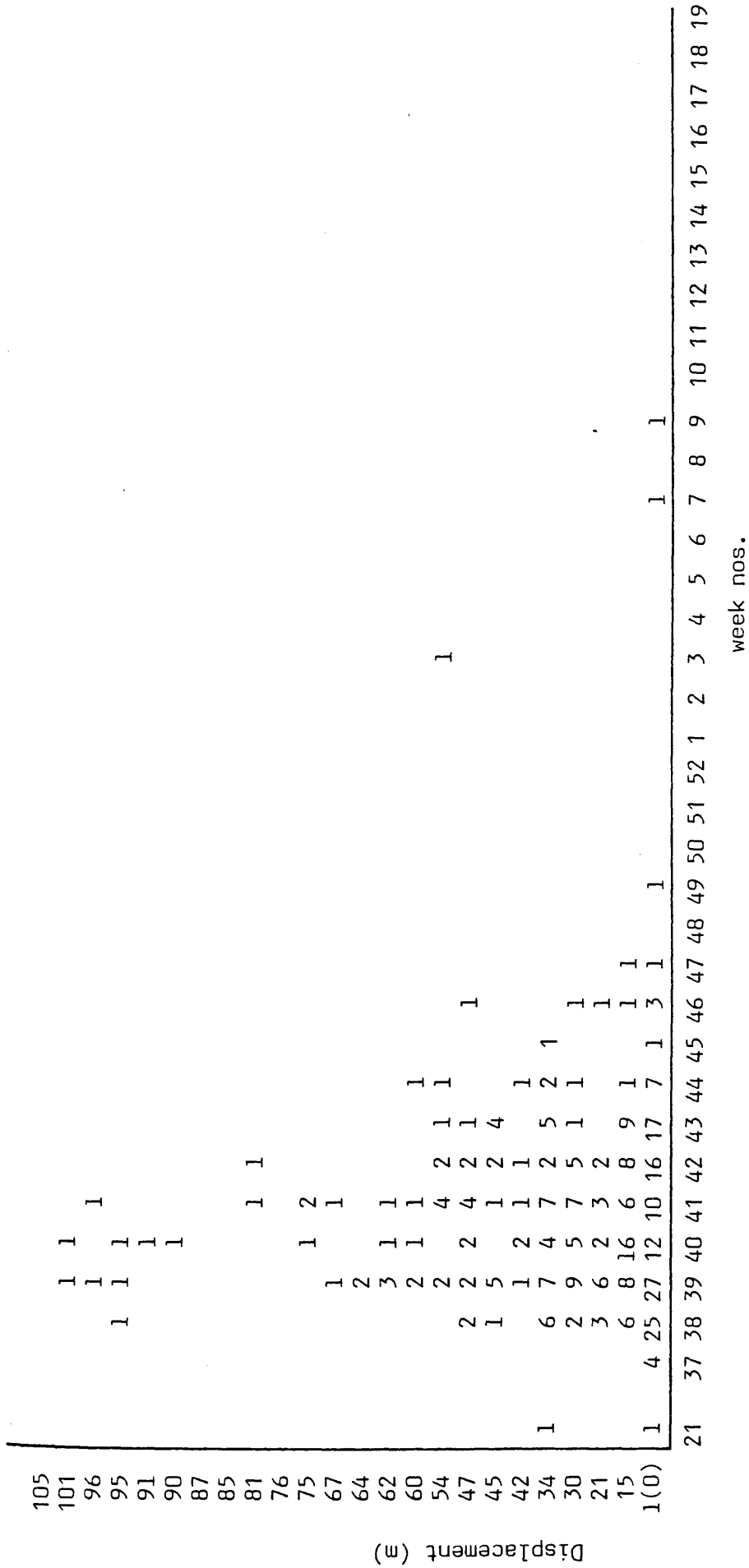


Fig. 5.8: *Nebria brevicollis* (ii): new generation beetles.
Change in displacement with season.

Table 5.16: Nebria brevicollis: Analysis of nett displacements
by subsequent recaptures, within 30 day periods
(figures from Figure 5.8 (ii))

Year	Month	Week Nos.	Number of recaptures	Sum of displace- ments (m)	Mean displace- ments (m)	Variance of mean	Standard error
1976	Sept	37/38	50	680	13.60	360.37	2.68
		39	78	2043	26.19	638.29	2.86
	Oct	40	50	1232	24.61	813.95	4.03
		41	50	1618	32.36	570.72	3.38
		42	41	811	19.78	402.33	3.13
	Nov	43	38	633	16.66	308.17	2.85
		44/49	26	498	19.15	410.13	3.97

being captured in the trap nearest to their release in the first few moments following their release. The mean displacement increases to a peak of 37.76m in 6-7 days, and then falls to a more or less steady level around the 30m mark. This levelling off is again an artefact: as time increases some beetles will begin to leave the grid area and so the larger displacements will be unrecorded.

Examination of the intervals between successive catches for the autumn of 1976 shows clearly an increase from a low mean value in mid-September (3.76 days) to 11.85 days in November (Table 5.15). An initial increase would be expected since large intervals are not possible at the beginning of the period. However, the increase persists throughout the autumn and so must be an indication of a gradual decrease in activity of the individual beetles.

Mean displacement is relatively low in mid-September (13.6m, see Table 5.16) but soon increases, reaching a peak of 32.36m in mid-October, before falling off again. Thus the high activity levels of late September are not associated with largest displacements. The peak in mean displacement coincides with the steady decrease in activity (see also Table 5.17 and Figure 5.9).

The overall picture is therefore one of low activity with little resulting displacement of individuals in space in the spring (overwintered beetles, and possibly the newly emerged adults as well) and, following the imaginal diapause, high activity, not immediately resulting in large displacements, but quickly building up before the activity begins to fall off again with the onset of winter.

Table 5.17: *Nebria brevicollis*: Change in rate of dispersal
with season.

Year	Month	Week nos.	No. of Individuals	Σ d/t (m/day)	Mean rate (m/day)	Variance of mean	Standard error
1976	Mar/May	10/18	23	35.83	1.56	3.54	0.39
	Sept/Nov	38/46	34	157.39	4.63	51.99	1.24

(i) Overwintered beetles

1976	May	21	2	34	17	512	16
1976	Sept	37-38	50	261.29	5.23	87.87	1.33
		39	78	790.50	10.13	150.44	1.39
		40	50	288.08	5.76	191.59	1.96
1976	Oct	41	50	273.18	5.46	39.63	0.89
		42	41	173.41	4.23	70.63	1.31
		43	38	86.87	2.28	10.53	0.53
1976	Oct/Nov	44/49	26	31.75	1.22	1.07	0.17

(ii) no evidence for overwintering

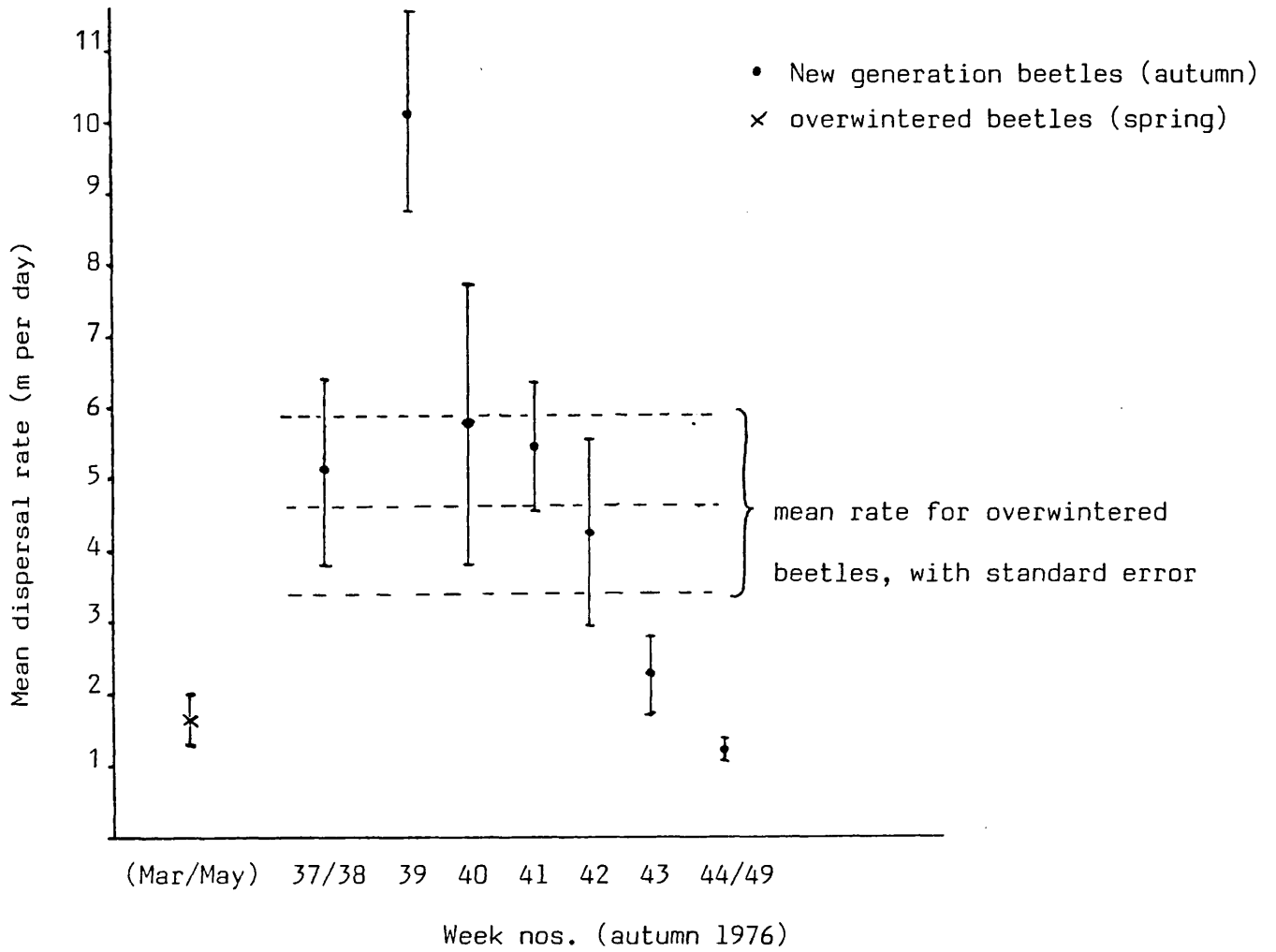


Fig. 5.9 Nebria brevicollis Dispersal rates in 1976.

In Figure 5.10 the percentage of recaptured beetles taken in traps away from the original trap of capture (and subsequent release) is examined with change in season. This shows the increase in displacement frequency in late September and early October already discussed. It also shows, however, that, whereas the frequency falls off again with the beetles which are not known to have overwintered, it remains high for the overwintered population. This is very interesting since it implies that the older beetles, which are in their second breeding season, wander further than those in their first season.

The direction of movements observed are shown in Figure 5.11. There is no evidence for any directional preference of the beetles (see Table 5.18).

Heterogeneity in the rate of dispersal of the individuals of the population may be detected by determining the departure from the normal curve of the frequency curve of numbers with distance from the point of release on a given day (Dobzhansky and Wright, 1943; Southwood, 1966). The departure or kurtosis was calculated on a daily basis (see Table 5.19) and the points plotted on a graph (Figure 5.12). From Figure 5.12 it can be seen that heterogeneity is present in the earlier stages of dispersal but that it gradually disappears with time. This is in agreement with earlier observations that some individuals disperse rapidly and soon leave the study area, and that the rest disperse at a slower, more or less constant rate.

Mason (1972) and Haines (1973) analysed their recapture results by examining the ratio between distance achieved and time duration per individual and termed the resulting statistics the 'Index of

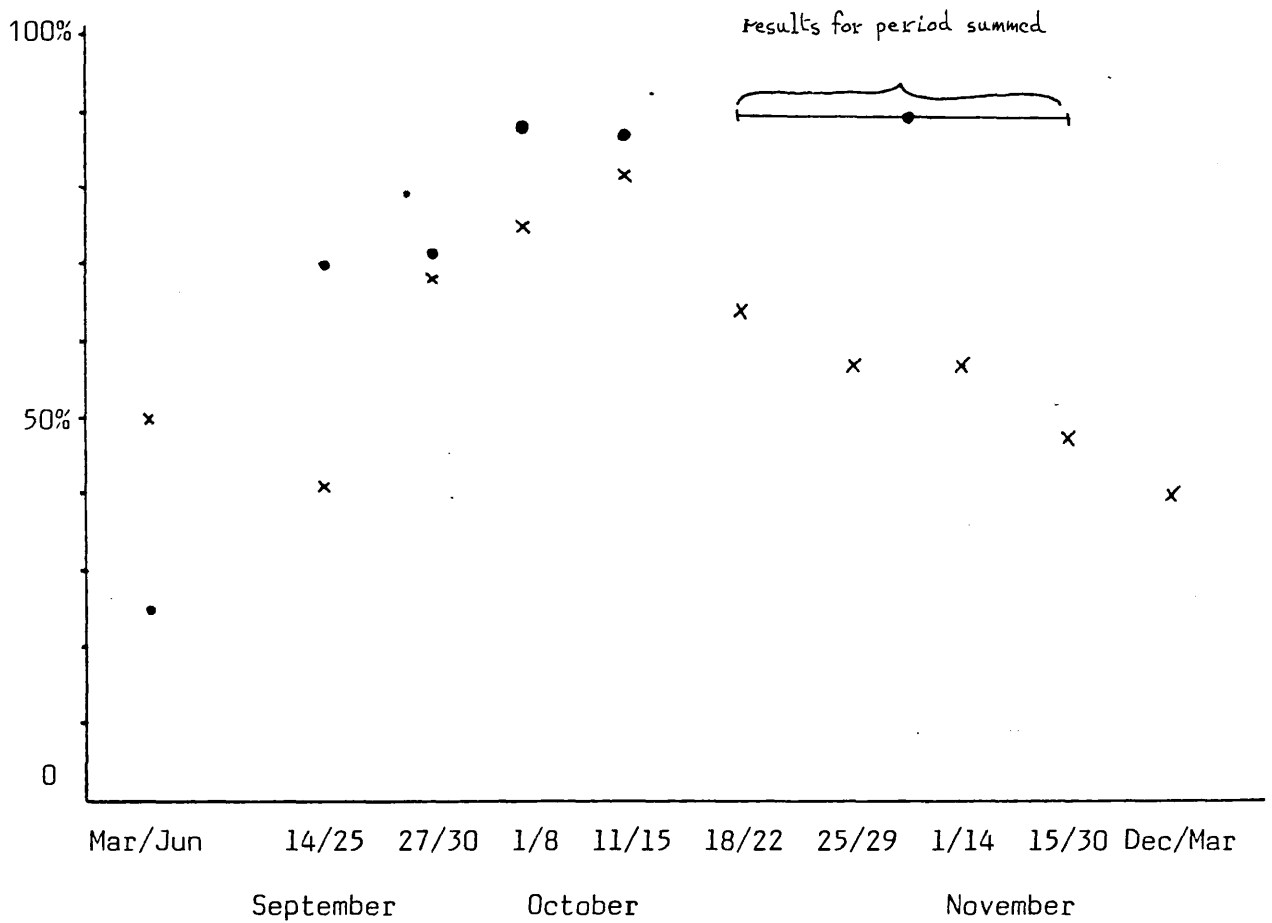


Fig. 5.10: *Nebria brevicollis* Percentage of beetles captured in a new trap during 30 day period. (• beetles known to have overwintered; x other beetles)

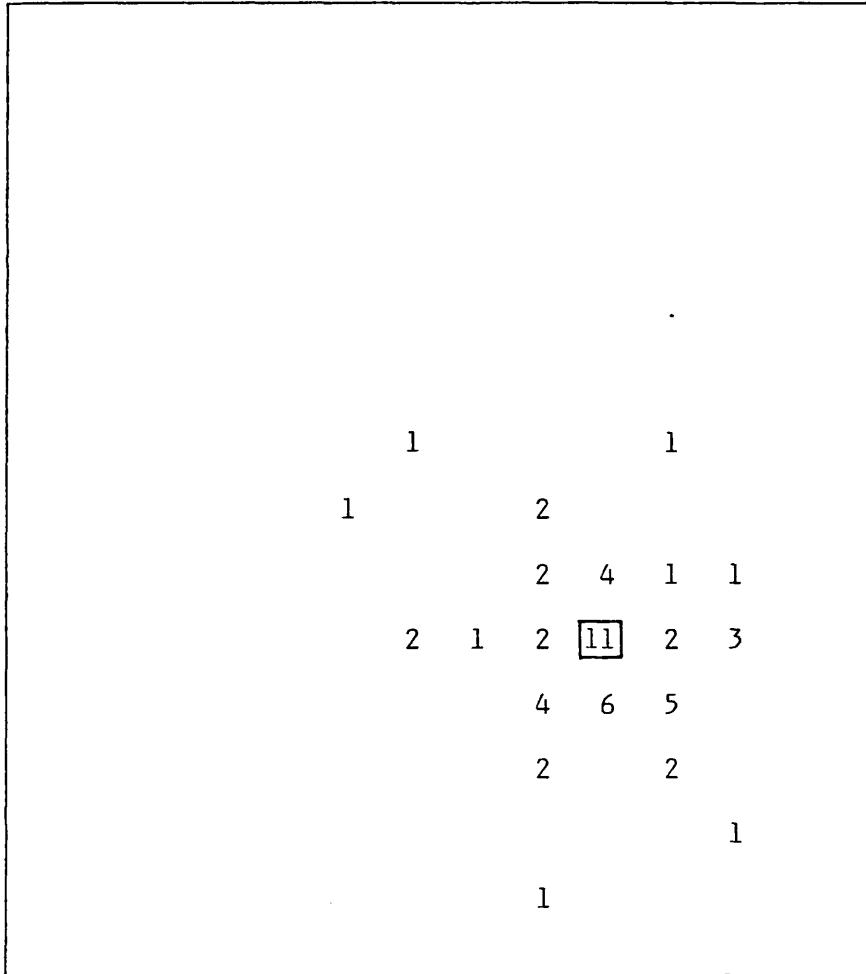


Fig. 5.11: Nebria brevicollis: direction of movements from release point Sept/Oct 1976

(i) Overwintered beetles

		2		1			1	1		
	1				1			1		
				2						
	1	1	2	5	5	4	2			
			5	4	7	1	1		1	1
	1	1	7	5	21	11	7			
1	2	5	16	29	160	30	12	5		1
	1	2	8	10	22	12	8	3	2	
1		6	1	5	12	10	3	1	1	2
		4	2	1	4	3	2	2	1	
		1			3	2	1	1	1	1
					1					
			1							
					1					

Fig. 5.11 (ii) Adults excluding those known to have overwintered

Table 5.18: *Nebria brevicollis*: Direction of movements found by mark release recapture

(i) field axis of Figure 5.11 (ii) : χ^2 5.615, with 3 degrees of freedom
: 0.2>P>0.1

Direction of movement:-	Extent of movement (m)				Total Recaptures
	15	30	45	60+	
Towards field	53	42	22	8	125
Away from field	73	37	14	12	136
Total Recaptures	126	79	36	20	261

(ii) pine axis of Figure 5.11 (ii) : χ^2 4.283, with 3 degrees of freedom
: 0.3>P>0.2

Direction of movement:-	Extent of movement (m)				Total Recaptures
	15	30	45	60+	
Towards pine	68	43	19	13	143
Away from pine	53	20	20	10	103
Total Recaptures	121	63	39	23	246

Table 5.19: Nebria brevicollis: values of Kurtosis with time.

Time	Sample size	Kurtosis
1	102	9.516
2	26	2.331
3	12	4.342
4	13	2.206
5	20	5.472
6	15	1.949
7	18	2.288
8	25	2.345
9	8	3.159
10	8	2.054
11	6	2.753
12	11	3.422
13	10	2.160
14	9	2.424
15	7	1.967

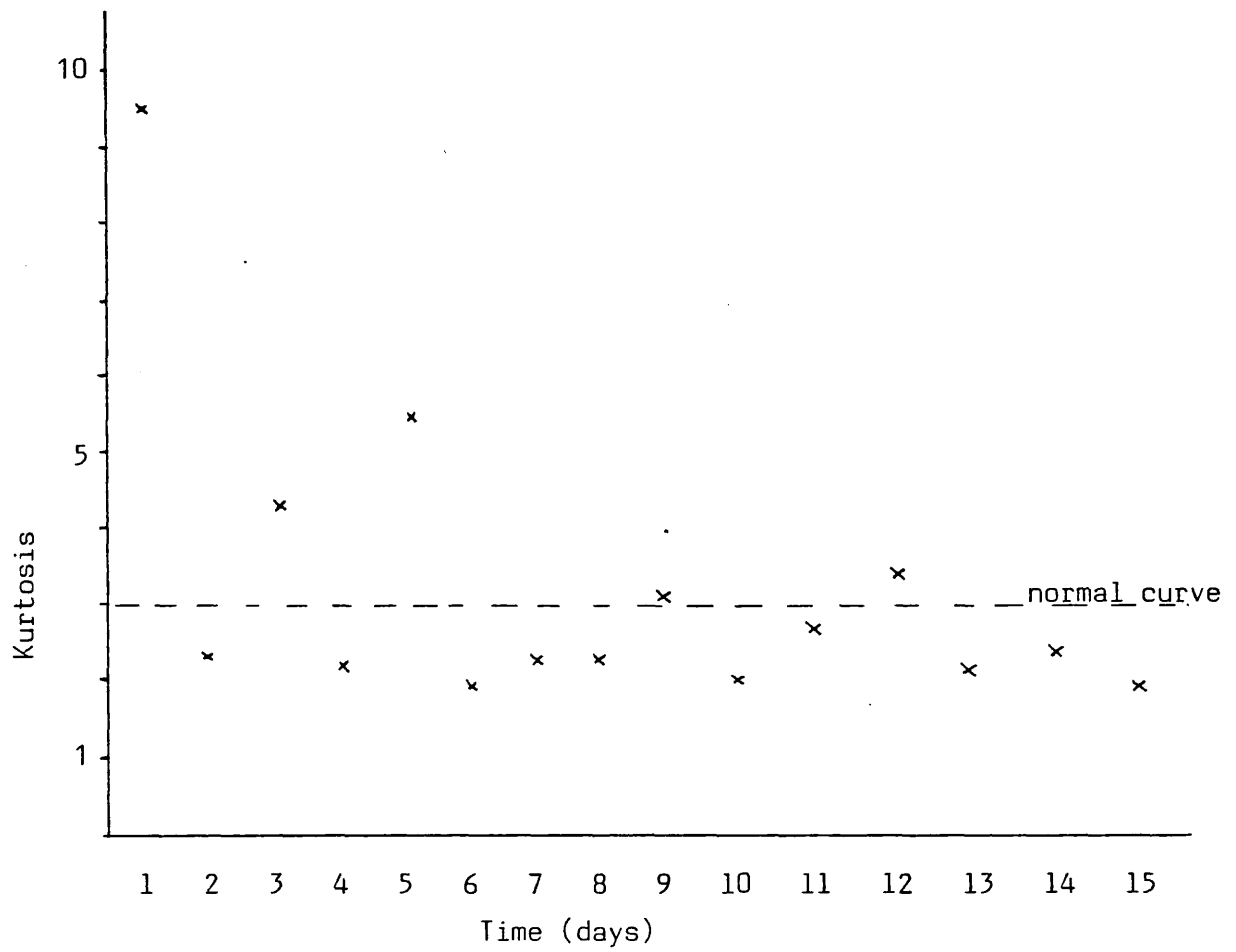


Figure 5.12: Nebria brevicollis: daily change in kurtosis.

the amount of movement', and the 'rate of dispersal' respectively. Mason (1972) however used the total figures for the calculation and not the individual figure. This is clearly of little use. For example, if one beetle has covered a large distance (D) in a short time (t), another a small distance (d) in a large time (T) then Mason's Index of the amount of movement is $\frac{(D + d)}{2} \times \frac{1}{(T + t)}$. However, Haines' 'rate of dispersal' is

$$\frac{\left(\frac{D}{t} + \frac{d}{T} \right)}{2}$$

The latter appears to be the most useful approach, and is therefore adopted in this study (Table 5.14 - mean displacement).

The mean rate of dispersal found by Tipton (1960) in mid October was 27 yds per 2 days (approximately 12.3m per day), and by Greenslade (1961) was 85 yds per week (approximately 11.1m per day). These compare favourably with the peak rate of dispersal of 10.13m per day in late September in this study (see Table 5.17). Tipton's fastest beetle was recaptured 75 yds (68.6m) from its release point after two days. In this study one Nebria achieved 90m in one night!

5.353 Pterostichus madidus

The recapture results for this species (Appendix 5.2) are interesting for the relative lack of movement of the female beetle at all times of the year (Figs. 5.13 to 5.15), and of the males outside the breeding season (Figure 5.15). In Table 5.20, the figures for nett displacement are brought together and examined according to sex and whether or not the beetles are known to have overwintered. It can readily be seen that the two age categories behave similarly, and

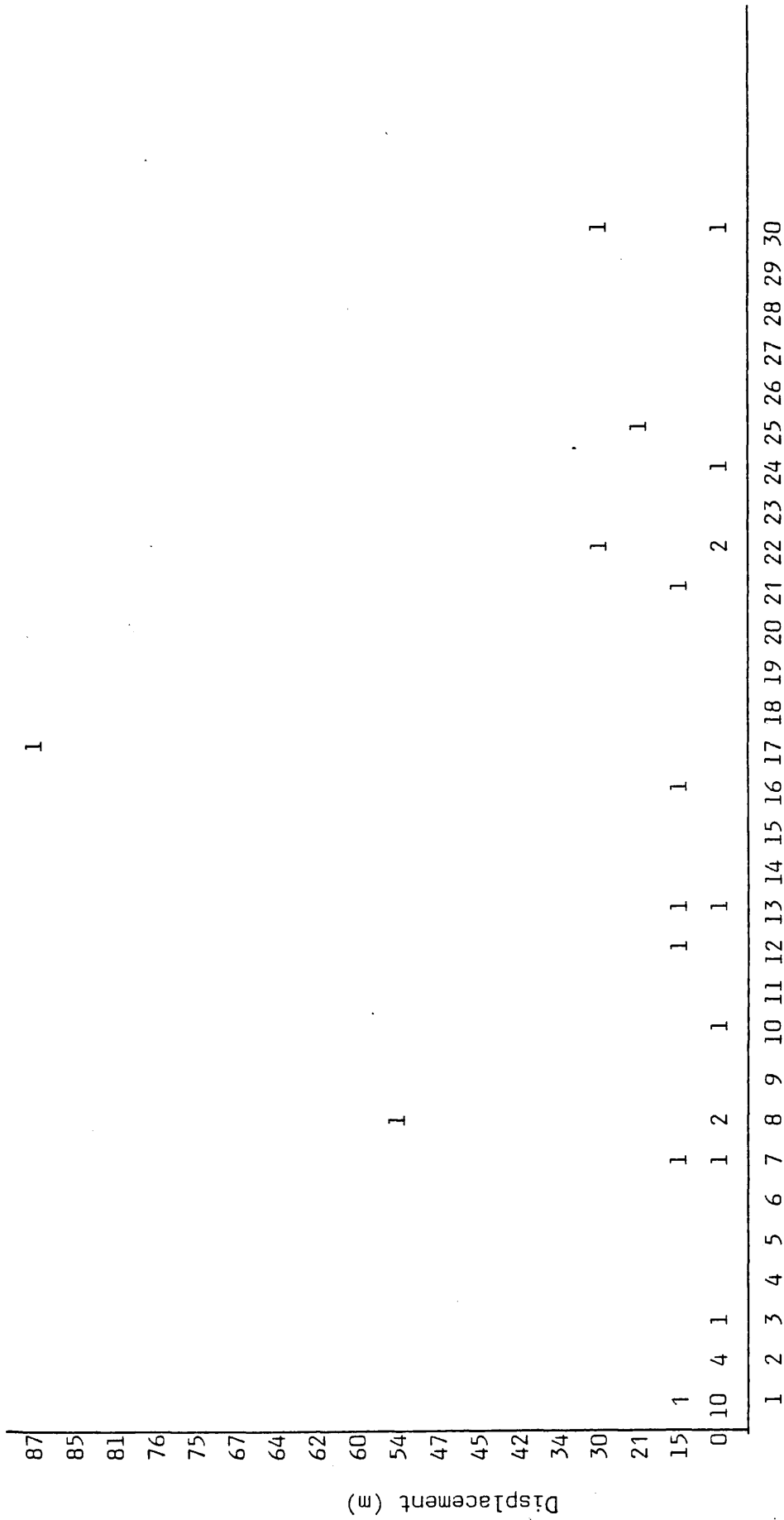


Figure 5.13: Pterostichus madidus : Displacements achieved within 30 days of release
 (i) ♂♂ beetles known to have overwintered.

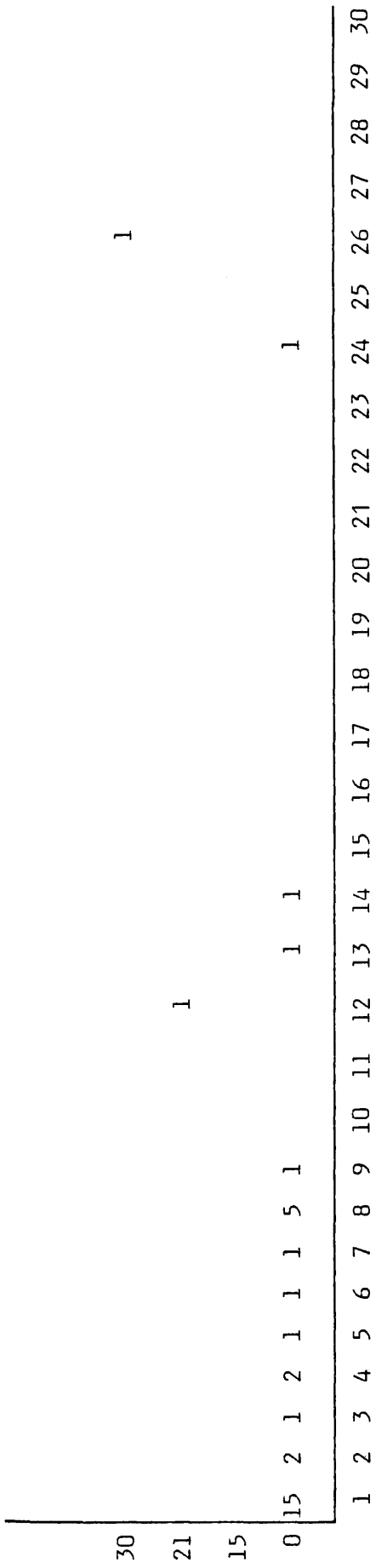


Figure 5.13 (continued)

(ii) ♀♀ known to have overwintered

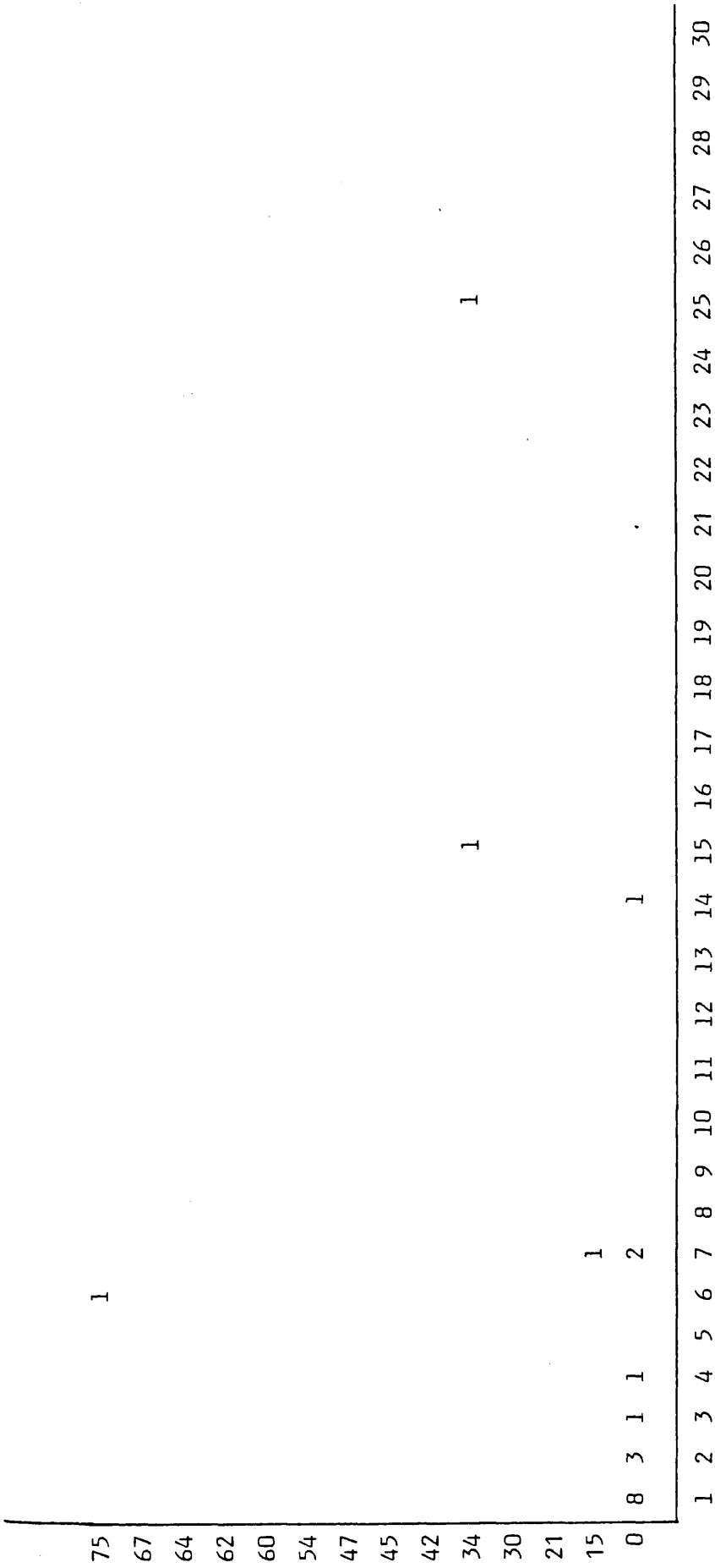


Figure 5.13 (Continued)
 (iii) $\sigma\delta$ excluding those in (i)

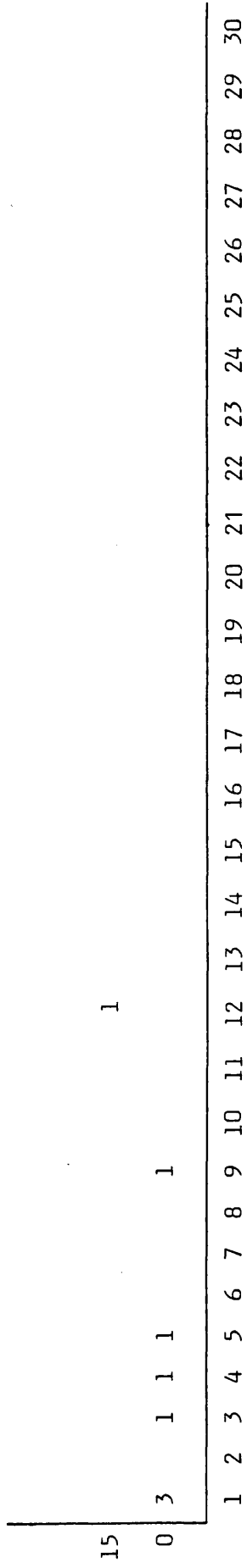


Figure 5.13 (Continued)

(iv) ♀♀ excluding those in (ii).

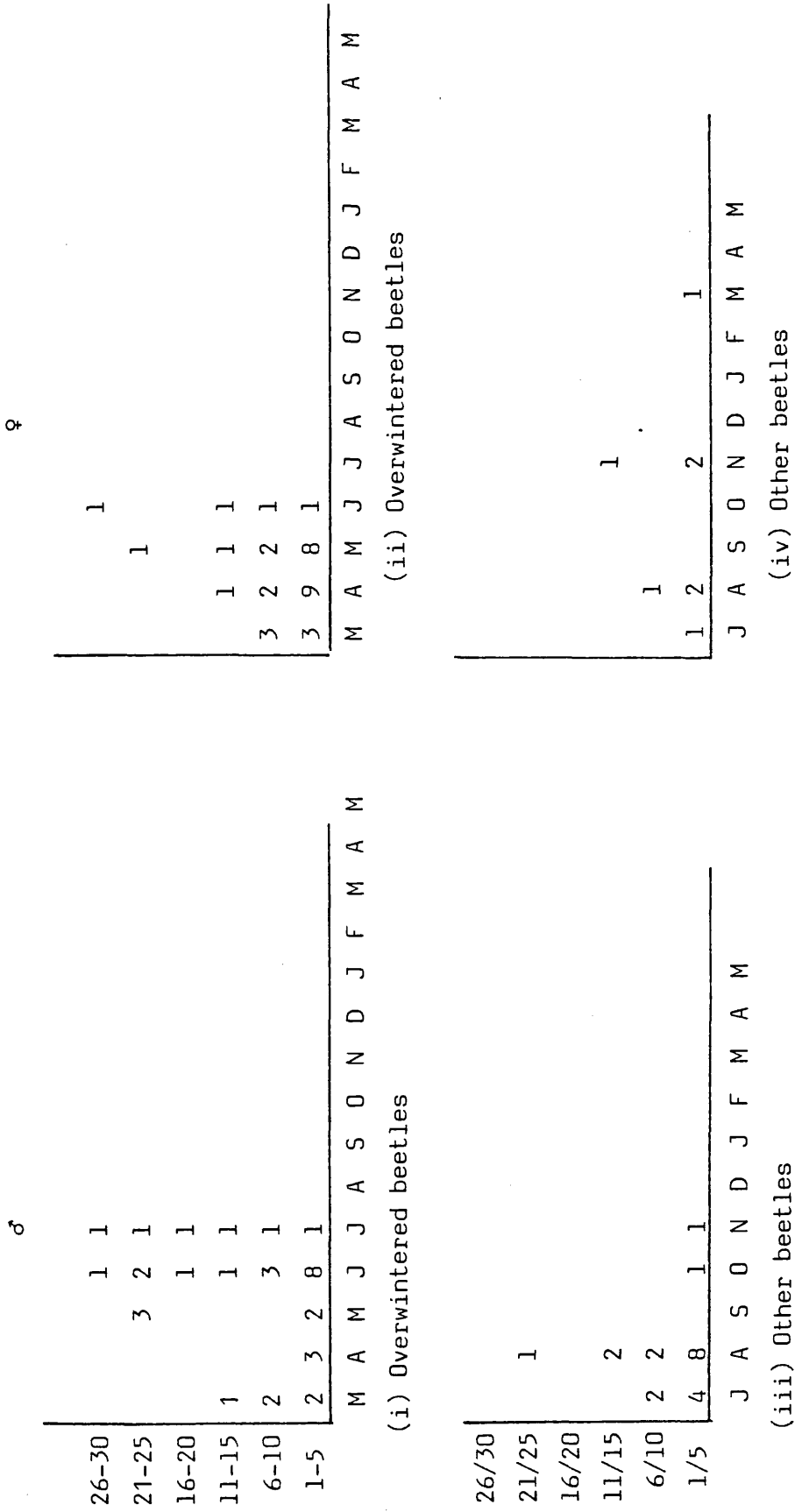


Figure 5.14 Pterostichus madidus: Change in recapture interval with season.

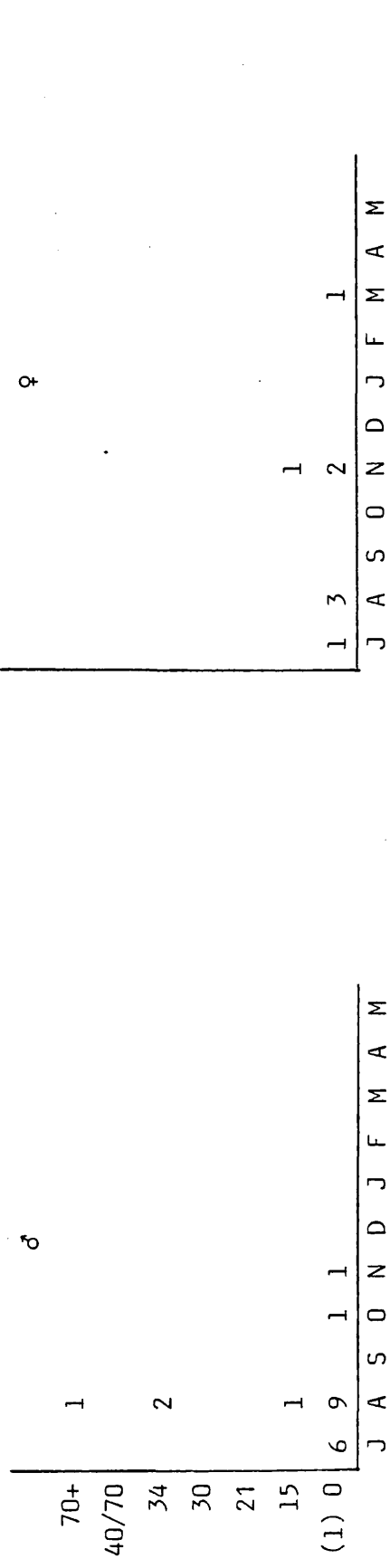
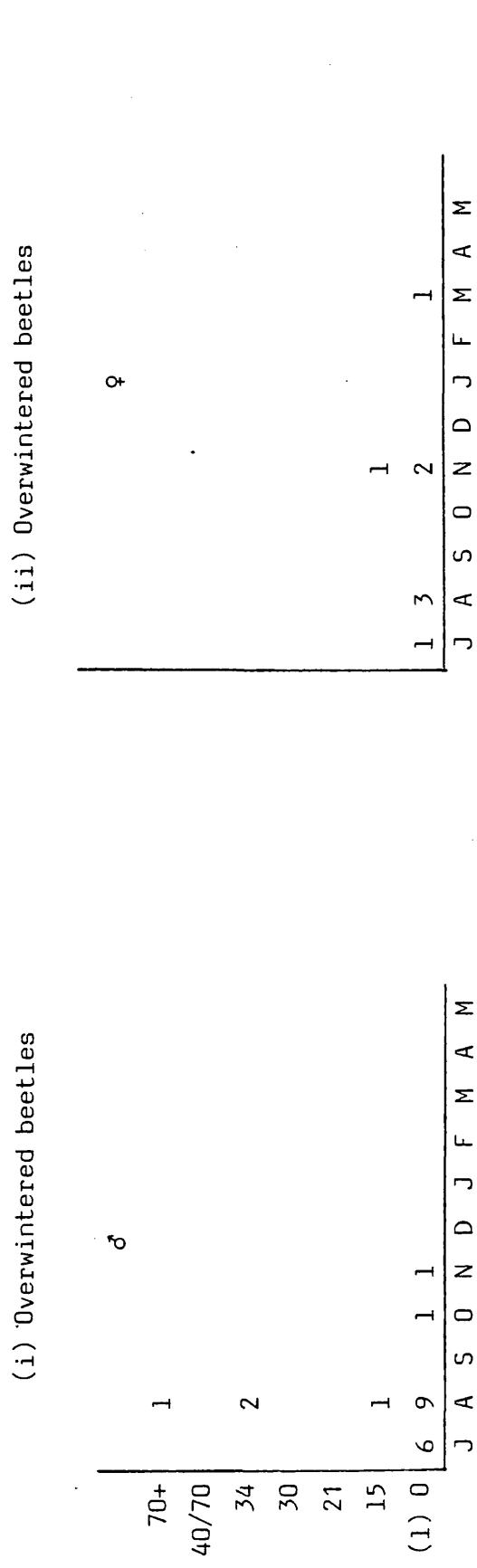
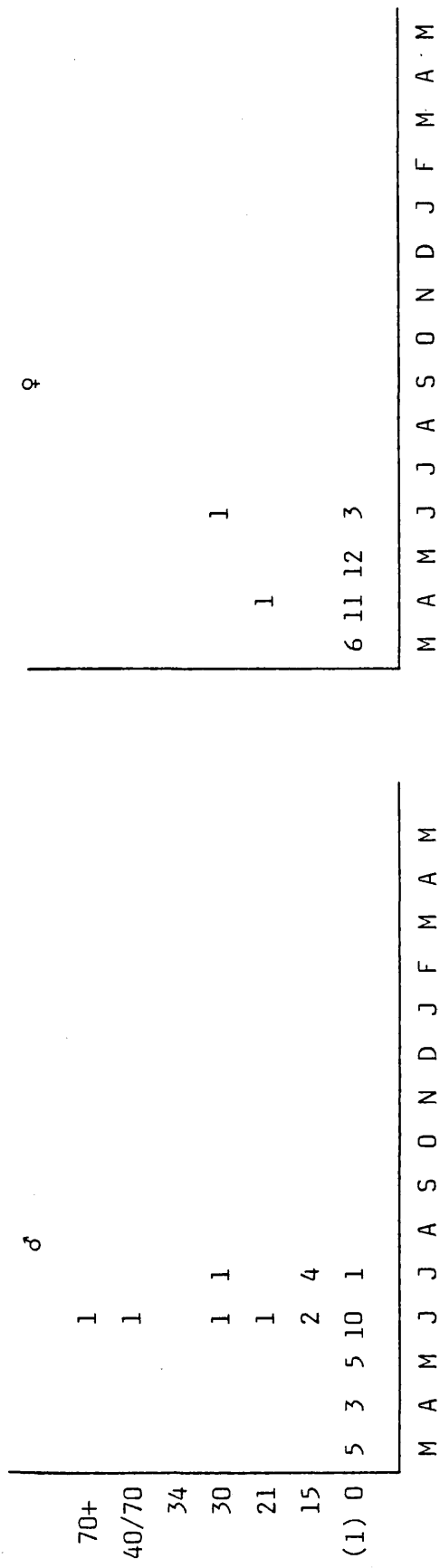


Figure 5.15: Pterostichus madidus : Change in nett displacement with season.

Table 5.20: Pterostichus madidus: Analysis of displacements
 achieved by the various beetles.
 (results from whole year)

	Number of recaptures	Sum of displacements	Mean displacements	Variance of Mean
Overwintered ♂♂	35	336	9.6m	319.8
♀♀	34	83	2.44m	35.46
All other ♂♂	20	174	8.7m	350.75
beetles ♀♀	8	22	2.75m	24.5

that the males generally travel further than the females.

A detailed breakdown of the displacement rate figures contribute to the understanding of the behaviour of the beetle (Table 5.21). The low dispersal rate of the female beetle is readily seen : the highest rate being during the small peak in activity of November (see 4.300). Male beetles similarly show low rates of dispersal, but with two notable exceptions: (i) the beetles which are known to have survived from the previous breeding season become highly active in June and July (see 4.300) and this coincides roughly with the increase in dispersal rate, and (ii) the beetles with no evidence of overwintering, and which are mostly the newly emerged generation, are not very active initially, but the dispersal rate soon increases to a peak in August and then falls. It is interesting that the two male dispersal peaks do not coincide - that the new generation males, although present, are not very active while the peak in dispersal of the overwintered males proceeds. Only when these older beetles have become less evident do the young males begin their activity peak. Dijk (1973) showed that the main period of reproductive activities of the two generations of Calathus melanocephalus occur in different parts of the breeding season.

Unfortunately the recapture results are not in the quantities found with Nebria and so detailed analysis is not possible.

The significance of the low dispersal rates now needs to be considered. Are they the results merely of low activity outside the breeding season in the males, and at all times for the females? With low activity levels there is a greater probability of capture

Table 5.21: Analysis of displacements with time during a 30 day period Pterostichus madidus (results taken from Appendix B).

(i) Male beetles known to have overwintered

Time of year 1976	Sample size	Total displacement (m)	Total time (days)	Mean d/t	Variance of mean
May-May	13	13	109	0.496 mdy ⁻¹	0.2
June	16	231	141	1.244 mdy ⁻¹	3.97
July	6	91	87	3.174 mdy ⁻¹	33.71

(ii) Female beetles known to have overwintered

Mar-May	30	50	137	0.627 mdy ⁻¹	0.212
June	4	33	49	0.585 mdy ⁻¹	0.326

(iii) Male beetles, excluding those known to have overwintered

July	6	6	21	0.520 mdy ⁻¹	0.156
August	13	165	77	1.941 mdy ⁻¹	10.41
Sept-Nov	2	2	7	0.292 mdy ⁻¹	0.0037

(iv) Female beetles, excluding those known to have overwintered

July-Aug	4	4	18	0.411 mdy ⁻¹	0.162
November	3	17	14	1.081 mdy ⁻¹	0.021
March 1977	1	1	4	0.25 mdy ⁻¹	-

in the nearest trap (i.e. the trap of the original capture in the case of marked beetles). However, the dispersal peaks do not follow the catch peaks precisely.

The clear-cut separation in dispersal rates of overwintered and new generation beetles is another indicator that something else is happening.

Activity is more or less high throughout the period April - August, so it seems unlikely that low activity can explain the dispersal rates by itself. The answer must be in the dispersive behaviour of this species, i.e. beetles are maintaining their location to particular areas of the site, and only during the breeding season do males, and males alone, wander freely within the site.

Greenslade (1961) could detect little emigration in woodland although he found movement of 36 yds in 4 days (8.23 mdy^{-1}) in grass heath. In garden habitats Nield (1974) found plenty of evidence of movement between sites - more so than in Nebria brevicollis! Mason (1972), working in deciduous woodland, found that the beetles moved at random in all directions and up to 17 metres per week (2.43 mdy^{-1}). This figure compares well with those found in this study for male beetles in the breeding season. None of the above authors separated male and female beetles for this analysis.

5.354 Abax parallelepipedus

As with Pterostichus madidus, the recapture rate for this species was rather low. Consequently the recapture results are too few for detailed analysis. Within the 30 day period following release of

marked beetles no individuals were recaptured in traps more than 33m from the release point (Appendix 5.3). Since pupal eclosion occurs throughout the summer months it is impossible in the majority of cases to separate the year age categories.

No significant increase in displacement with time could be detected within thirty days (Figure 5.16), and most of the displacements were found to occur early in the season (Figure 5.18). Although no females were found away from the trap of the original capture once the dubious results had been excluded from analysis (Fig. 5.9(ii)), examination of the results in Appendix 5.3 shows that females did disperse. Two recaptures of female beetles were made away from the release point: at 15 and 21 metres. Both of these were captured over a weekend and so the time intervals were between 1 and 4, and 1 and 3 days respectively. As with the males, these were early in the season. The only late season male showing dispersal was a callow beetle which was captured 15m from its release point after two days.

Greenslade (1961) described this species as exhibiting extensive migration. However, his conclusion was based solely on the low recapture rates obtained. This study also produced low recapture rates, but also low displacements.

Mason (1972), whose analytical approach has already been mentioned (5.352), found that dispersal in this species was random in all directions and increased in rate with season : July, 2.9m/beetle/week; Aug/Sept, 4.2m/beetle/week; September 6.4m/beetle/week.

5.355 Carabus violaceus

Within the 30 day period only four C. violaceus were recaptured,

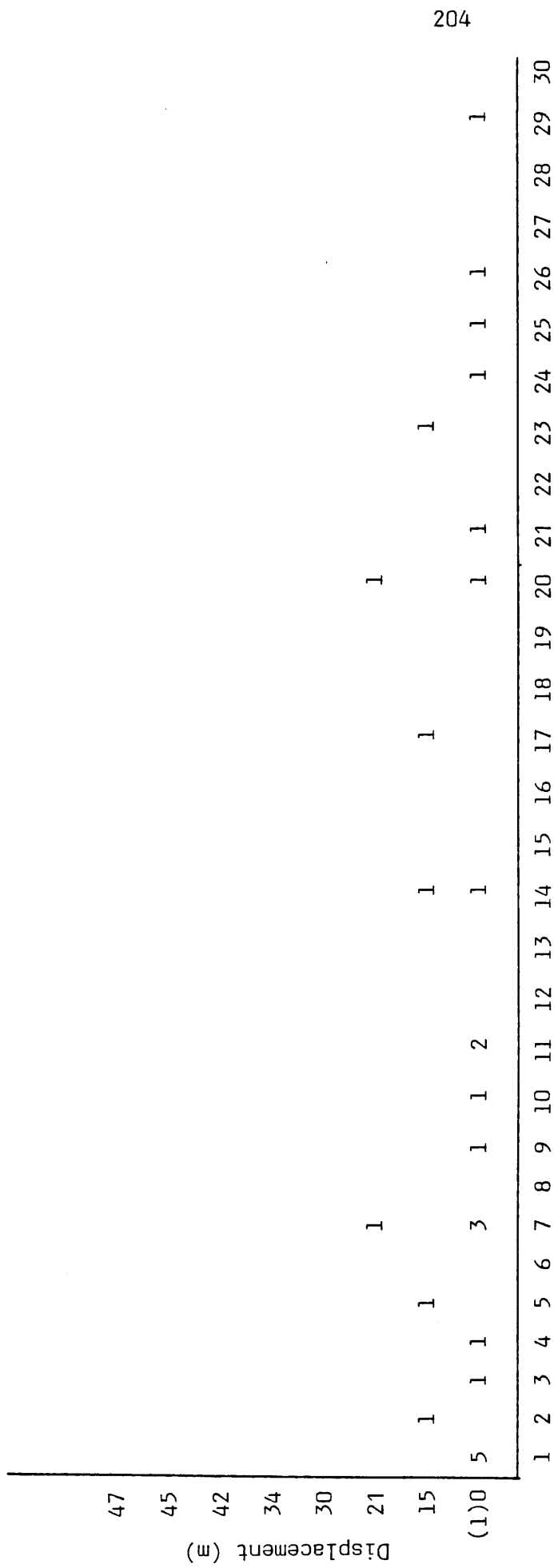


Figure 5.16: Abax parallelepipedus, males : displacement rate within 30 days of release
 [28 recaptures; mean displacement 4.93m variance 53.89]

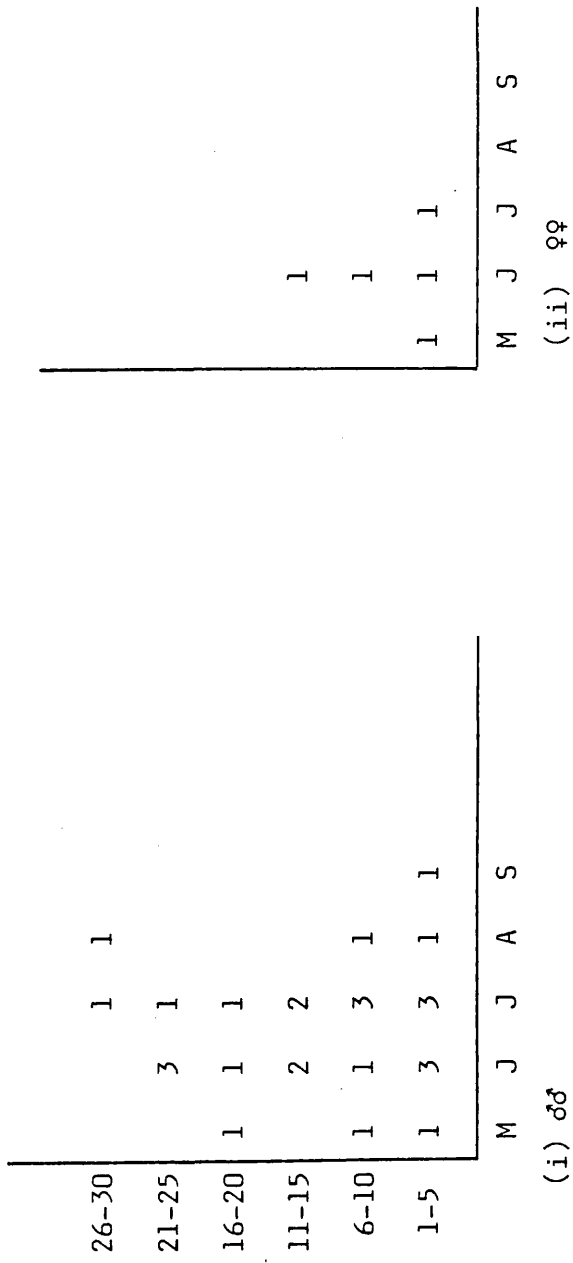


Figure 5.17 Abax parallelepipiedus: change in recapture interval with season

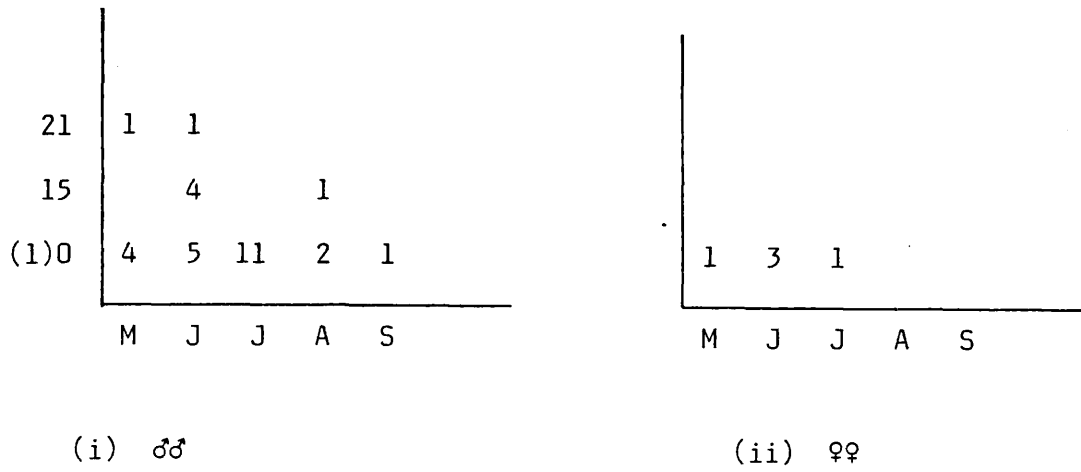


Figure 5.18 Abax adults : change in nett displacement with season.

and three of these were captured during weekends. A male beetle, which had probably overwintered, was captured in the trap next to the release point after 11-13 days, and another, callow, male was found, in the same trap again, after 4-6 days. The other two captures were female beetles and both were captured in new traps: one at 21m after 17-19 days, and the other at 15m after 2 days. The latter beetle was callow.

Only two more beetles were captured outside the 30 day period: a male at the same trap after 30-32 days, and a female at 33m after 42 days. Thus with six recaptures, three females have all dispersed, and the three males have not. However, a male which was trapped outside the main study area (at H4 location) was recaptured 24 days later 42m away from the release point. So displacement does occur in males.

Little can be said, therefore, about dispersal in this species at this stage in the investigation. The fastest movement was the callow female at 15m in 2 days.

The mobility of this species has not been investigated by other authors.

5.356 Pterostichus niger

As with Carabus violaceus, few recaptures were made. A single female was recaptured at 30m after 48 days, on July 20th, and three males were recaptured, all in the original trap, after 4-6 days, 11 days and 20 days. This situation is identical with that in C. violaceus - the only displacements registered were in the females.

Dispersal in P. niger has not been studied by other workers due

mainly to the sparse populations and low recapture rates.

5.357 Other species

Captured specimens of twelve other species were given individual marks during the course of this investigation. The results are not analysed or used in any of the following discussions, but are presented in the Appendix (5.4) for information only.

5.360 Density effects

5.361 Introduction

Grüm (1962), studying the horizontal distributions of larvae and adult ground beetles in Polish pine forests found a negative correlation between their respective numbers at the various sites studied. He concluded that female beetles must migrate from feeding areas to oviposition sites. The species studied included Carabus violaceus and Pterostichus niger, although the effect was most obvious in other species (see also 5.320).

In contrast to this breeding movement, Haines (1973) found that Nebria brevicollis and Abax parallelepipedus showed a tendency to remain in those parts of the study area in which their total adult catches were relatively high, i.e. movements were found to occur more in the peripheral areas of the population distribution. The highly aggregated distributions of Nebria beetles are well known (e.g. Greenslade 1961, Drift 1951).

Here then are two conflicting viewpoints: (i) some species migrate to oviposition sites and thereby move away from high adult densities, and (ii) other species tend to remain in areas of high

density, and most movement occurs in the areas of low density. It is the aim of this section to examine such density effects.

Earlier in this chapter (5.320) changes in the distribution of the beetles with season were examined in Nebria brevicollis and Pterostichus madidus, and found not to occur in the former. However, no definite positive correlation was found between pre-oviposition and oviposition distributions in P. madidus. It was therefore suggested that Grüm's conclusion may apply in this species. Since then, however, it has been shown that little dispersal occurs in the females (5.357) and so migration to oviposition sites seems very unlikely.

5.362 Examination of the Results

The basic approach was to compare the recapture results with the catch totals at the individual trap level. Nebria brevicollis adults were recaptured in large numbers and so more detailed analysis was possible (Tables 5.22, 5.23, Fig. 5.19). The general picture was that the mean of the distances achieved between subsequent captures decreased with the size of the total catch. The results used were from September to November 1976. Beetles captured in traps producing less than 40 adults in the autumn tended to be recaptured at greater distances from the trap of the first capture than those taken in traps with larger catches, (χ^2 14.437; 7 degrees of freedom : $0.05 > P > 0.02$). This effect is clearly seen in Figure 5.19.

Pterostichus madidus results were examined for the whole year, but recaptures with zero nett displacements were not included because of the large percentage of animals which are normally static (Table 5.24 and Figure 5.20). As with Nebria mean distance of recapture

Table 5.22: *Nebria brevicollis* frequency distribution of displacements achieved by subsequent recapture according to catch size of origin (all adult beetles Sept - Nov 1976).

Catch Range per trap	Distance achieved by next capture (m)																				Total beetles released	Number recaptured	% Recapture	Mean distance	Variance	S.D.					
	0	15	21	30	34	42	45	47	54	60	62	64	67	75	76	81	85	87	90	91							95	96	101	105	136
1-20	10	3	4	6	6	1	1	1	1	1																248	37	14.92	31.27	989.9	31.46
21-40	10	7	5	2	6	1	3	2	1		2	1								1	2					217	44	20.28	32.32	840.4	28.99
41-50	23	11	5	3	4	1	3	5	1	3	1															265	61	23.02	22.70	538.9	23.21
51-55	26	13	10	7	14	2	1	3	6	2	2	1	1									1				363	89	24.24	26.25	570.2	23.88
56-60	16	6	5	2	1	1	1	1	2																	173	35	20.23	17.2	431.0	18.50
61-70	7	9	5	5	4	3	2																			201	37	18.41	23.65	285.7	16.90
71-80	19	3	2	4	1	3	1	3	1	1																156	39	25.0	20.82	582.7	24.14
81-90	17	20	6	3	8	1	3	5	3	2	2	1	1													339	72	21.24	24.57	405.4	20.14
91-100	4	9	3	2	8	1	1	1																		187	31	16.57	24.74	338.1	18.39
101-150	27	8	2	3	4	2	7	3	1	1																346	59	17.05	20.05	498.8	22.33
151	20	29	5	14	7	2	3	3	1																	302	84	27.81	19.52	182.1	13.50
229	22	8	1	6	3	1	3	1	1	1	1	1														229	51	22.27	22.39	664.2	25.77

Table 5.23: Nebria brevicollis: results from Table 5.22 treated as an 8 x 1 Contingency Table

($\chi^2 = 14.437$; with 7 degrees of freedom $0.05 > P > 0.02$)

Catch Range	Distance achieved (m)								Total
	0	15	21	30	34	42 to 54	60 to 85	87 +	
1-40	20	10	9	8	12	9	6	7	81
41-80	91	42	27	21	24	29	22	4	260
Total	111	52	36	29	36	38	28	11	341

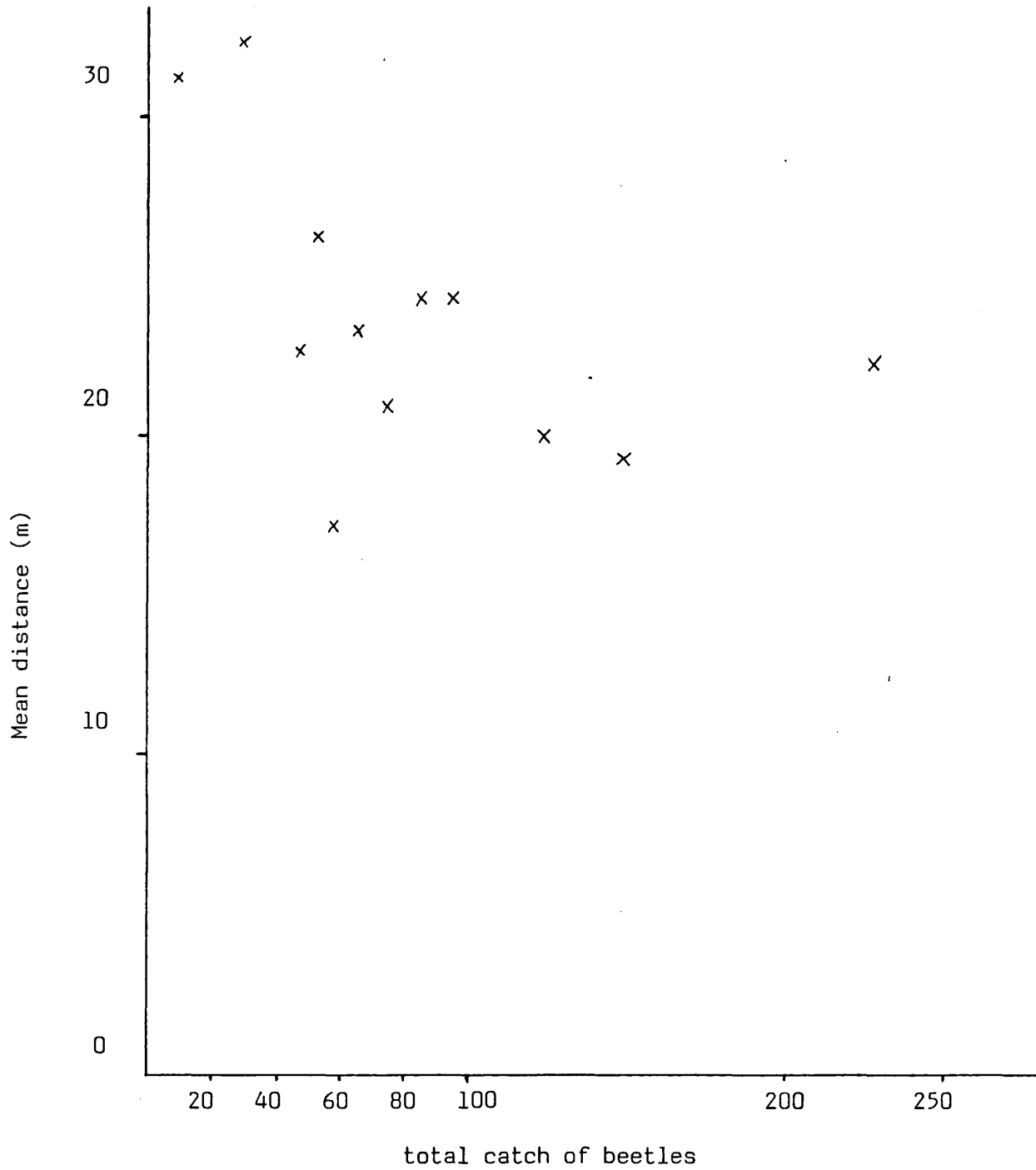


Figure 5.19: *Nebria brevicollis*: Mean distance achieved between captures according to catch size category of trap of origin (all adult beetles included, Sept - Nov 1976).

Table 5.24: Pterostichus madidus (males): frequency distribution of displacements achieved by subsequent recapture, according to size of original monthly catch (all adults).

Catch Range	Distance achieved between captures (m)																Total Recaptures	Mean distance						
	15	21	30	34	42	45	47	54	60	62	64	67	75	76	81	85	87	90	91	95	96	106		
1-4	4	3	2	2	1	1	1	1					1		1		1						17	38.82
5-8	8	2		3	1	1	1	1				1									1		18	32.67
9-14	4	2	3	2	1									1									13	29.46
15-29	8	2	3		2												1						16	26.81

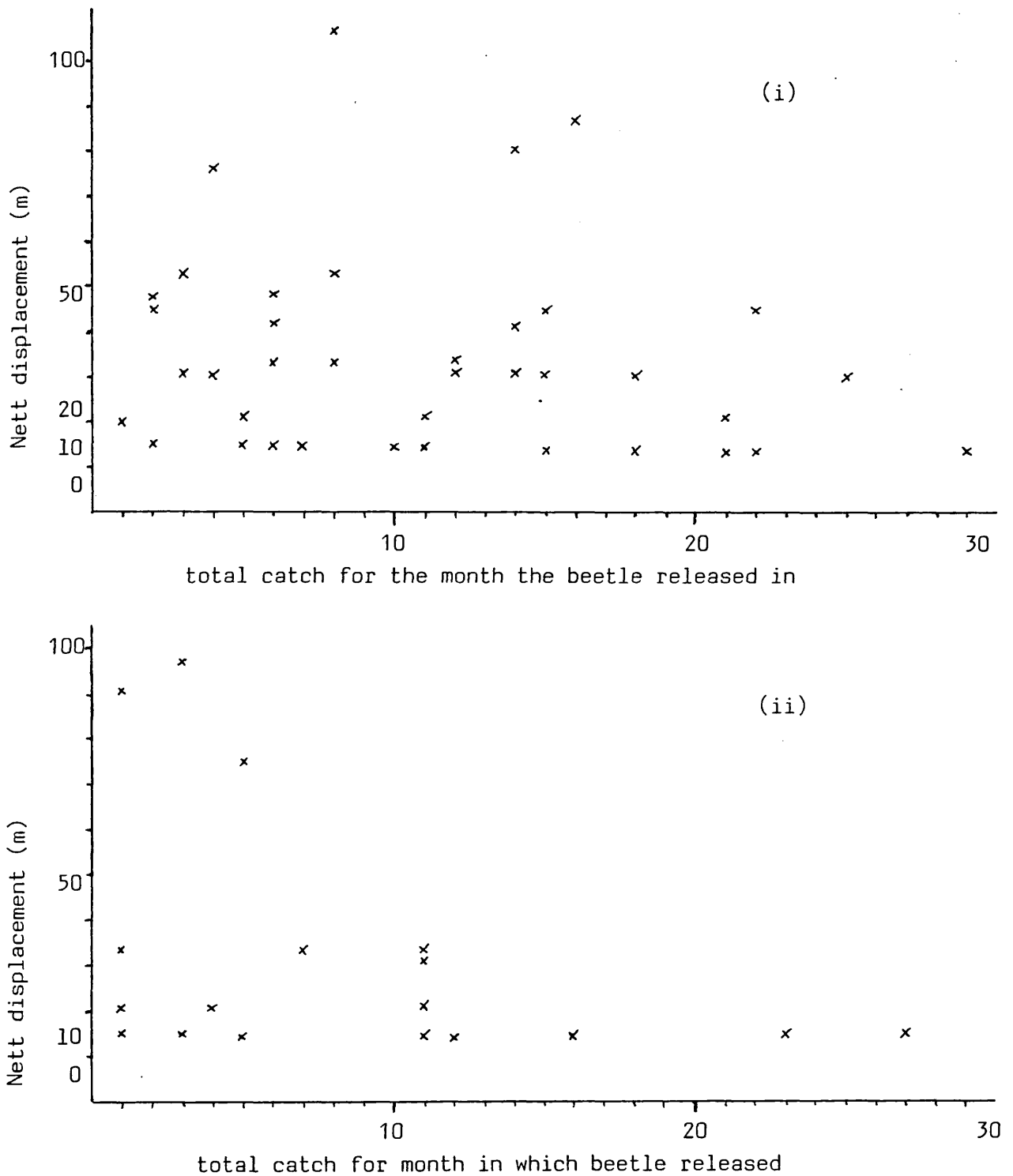


Figure 5.20 Pterostichus madidus: Scattergrams showing relationship between size of catch and subsequent dispersal (i) overwintered adults, (ii) new generation

decreased with the trap monthly catch size.

Abax parallelepipedus produced a similar result (Figure 5.21). Therefore the observation made by Mason (1962), that the beetles tend to remain in the areas producing the largest catches, is confirmed.

5.370 The source of unmarked beetles in the study area

In an intensive marking study such as this it is of interest to see where new individuals are coming from. Once past the period of pupal eclosion the only source of new beetles within the grid area must be from the surrounding area. Therefore one would expect that most unmarked beetles would be caught at the periphery of the grid during this time. However, if the traps are at too low a density to sample fully the parts of the populations within the grid, the source of unmarked beetles will be the study area itself. Thus two extreme positions can be envisaged resulting in distributions of unmarked beetles around the edge of the grid, or evenly spread within the grid. The greatest difficulty is that high rates of movement allow greater penetration. However, the pattern of diffusion would still be expected to show up in analysis.

The approach to this problem was to use Spearman's Rank Correlation Coefficient (described earlier 5.320) to compare the distributions of marked and unmarked beetles at a time when the appearance of callow adults has ceased. Abax results could not be analysed since callows are present throughout the summer (see 4.400).

The combination of large numbers of ties with low numbers of beetles puts the validity of the test in question. However, the

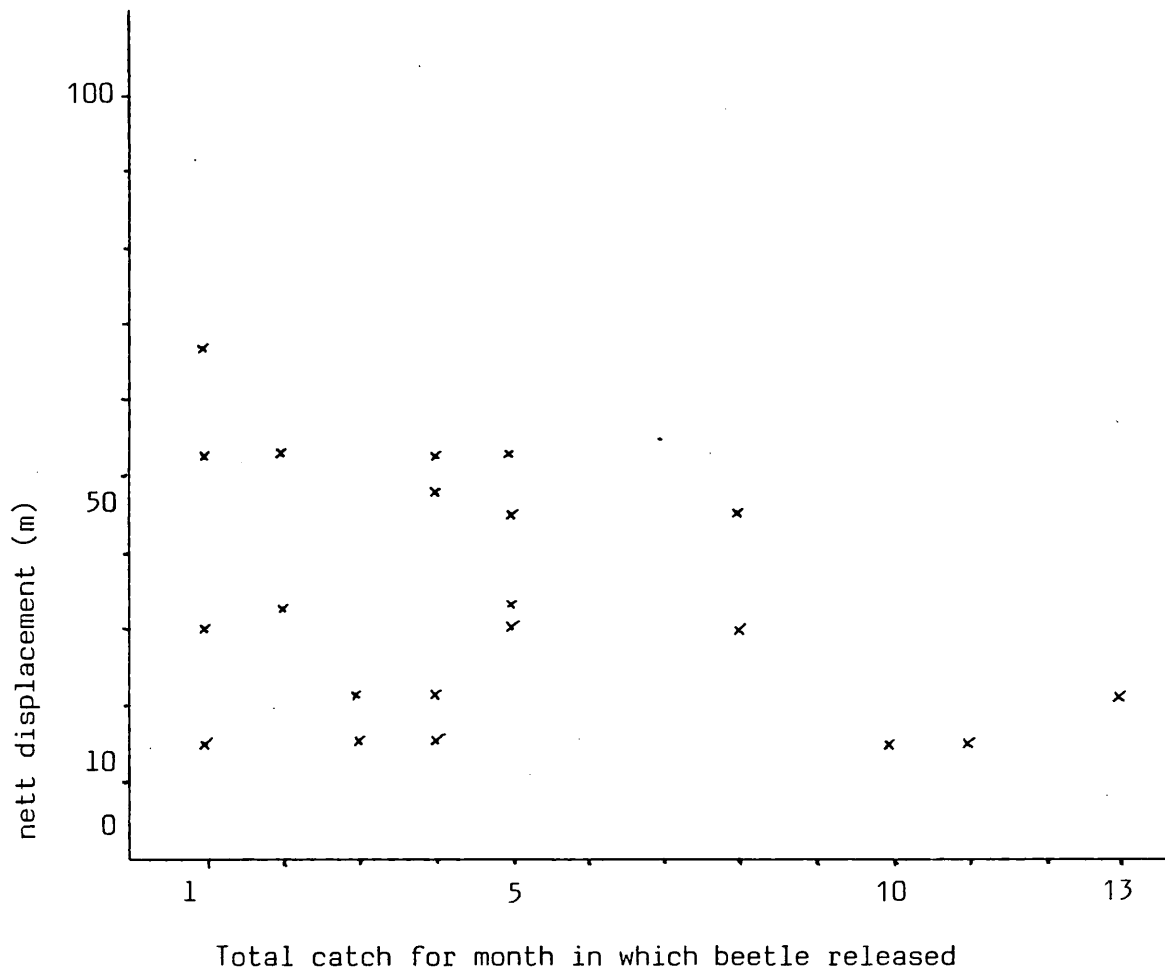


Figure 5.21: Abax parallelepipedus (males): Scattergram showing relationship between size of catch and subsequent dispersal.

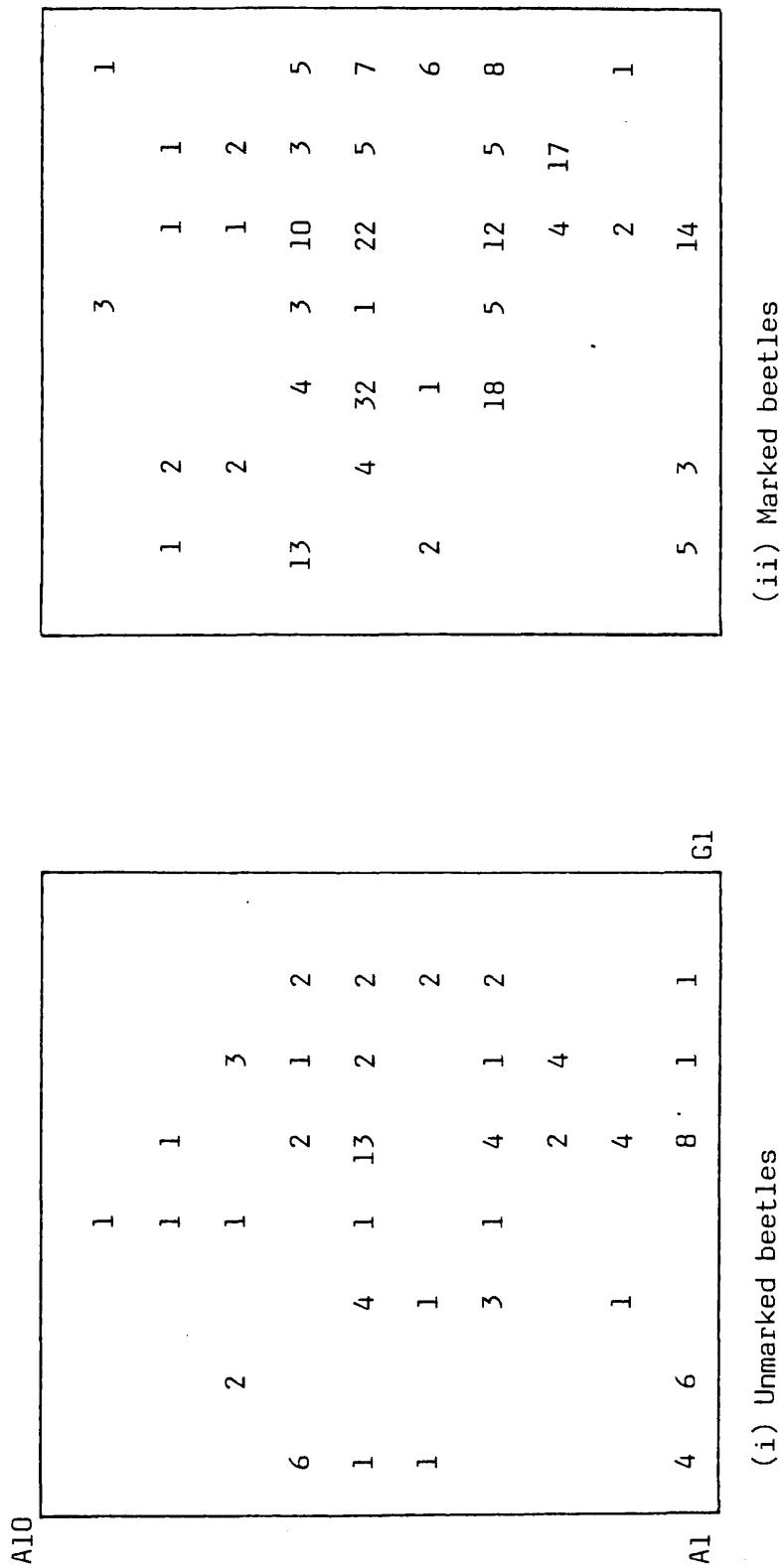
Nebria results (Figure 5.22) were found to have a significant positive correlation ($r_s = +0.657$, $P < 0.001$), and so it seems unlikely that the major source of unmarked beetles is in the surrounding area. With Pterostichus madidus a positive correlation was found, but not significantly so. (Figure 5.23, $r_s = + 0.224$, $0.10 > P > 0.05$).

Visual examination of the distributions of unmarked and marked beetles for both species (Figs 5.22 and 5.23) does confirm the conclusion that unmarked beetles are not coming solely from the boundary of the study area.

5.380 Estimation of the abundance of the beetles

It was pointed out in Chapter 3 that, although the activity levels of the beetles will be extremely variable, the actual abundance will be much less so. The peak abundance of adult beetles corresponds with the peak in emergence of the new generation from their pupal cells. After this there is constant loss of individuals through mortality and emigration, which is only partly compensated for by immigration. Thus numbers decrease steadily from the peak emergence time.

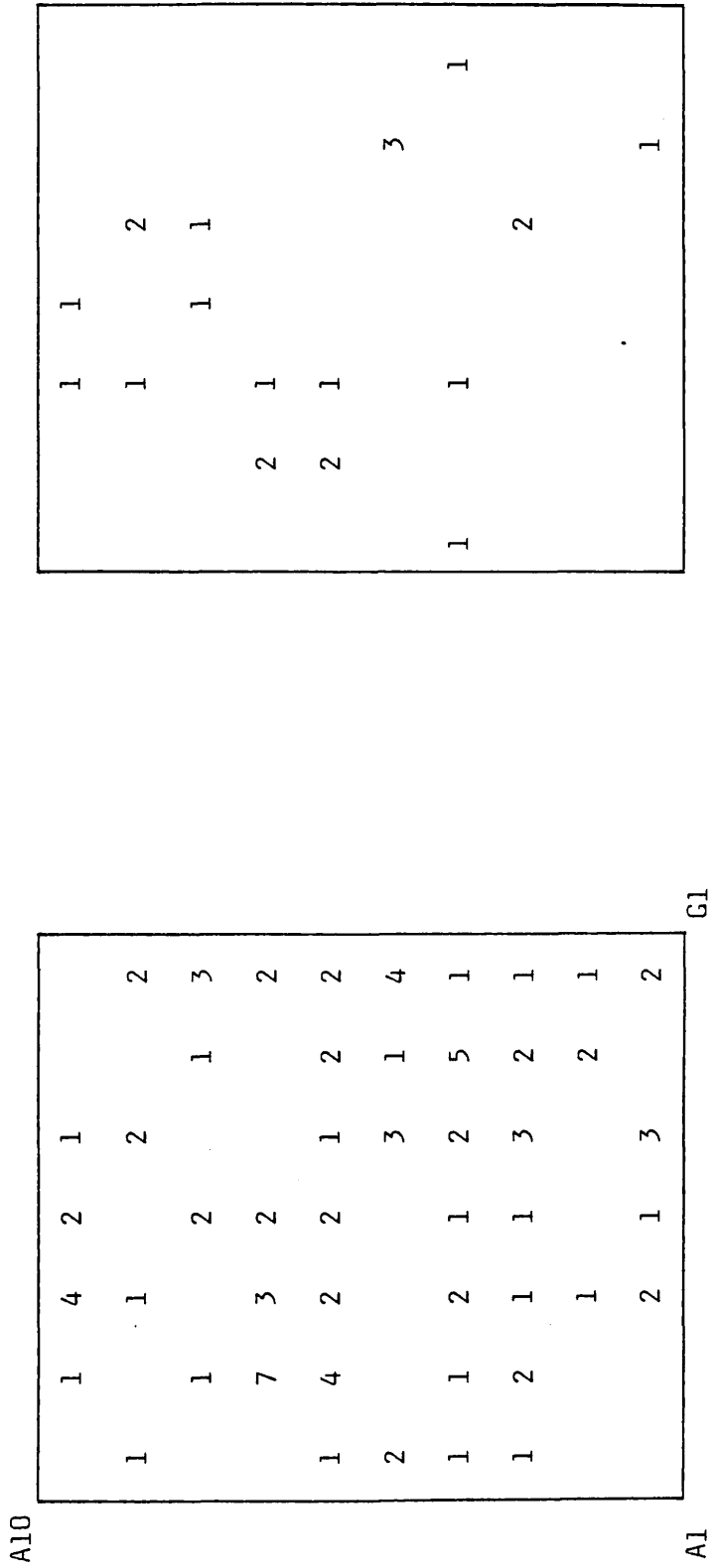
The best time to estimate the numbers of beetles present in an area is the period of highest activity, when one is most assured of the intermixing of marked and unmarked beetles. The population density estimation techniques which have been devised are all based on a number of assumptions. Unfortunately some of these assumptions are questionable (see, for example, Southwood's (1966) discussion of the validity of the assumptions). A good approach is to use more than one method to estimate the population density and to compare the results.



(ii) Marked beetles

(i) Unmarked beetles

Figure 5.22 *Nebria brevicollis*: distribution of captured beetles in the study area November 1976 until March 1977. (r_s 0.657, $r = 7.18$ with 68 degrees of freedom. $P < 0.001$)



(i) Unmarked beetles

(ii) Marked beetles

Figure 5.23 Pterostichus madidus: distribution of captured beetles in the study area. Nov 1976 - March 1977.
 (r_s 0.224, $t = 1.8931$ with 68 degrees of freedom : $0.10 > P > 0.05$)

The Jolly-Seber method (Jolly 1965, Seber 1965) was applied to the results for Nebria brevicollis during its peak of activity following diapause (Tables 5.25 - 5.27). This method is the most appropriate one available for use in studies involving three or more successive samples (Southwood 1966). Although the results for this study are based on only five successive days sampling each week, Parr (1965) points out that the time intervals between successive samples do not need to be equal, as long as the length of each sampling period is constant.

Nebria was selected for this calculation since it is the only species found to have a large recapture rate, high mobility and many multiple recaptures. As can be seen from the final table (Table 5.27), the daily population estimates are very variable. This is a reflection of the relative inflexibility of statistical models when applied to biological situations. Inactive beetles can only be registered when they become active again.

The highest estimate is for September 28th, and is of 1563 adults. The grid is of 7 by 10 traps spaced at 15 metre intervals, and so may be considered as covering an area of 15,750m². This gives an estimated density of 0.1 beetles per m², or one beetle per 10.08m². This is very low. However, it must be remembered that the Nebria population is highly aggregated within the study site.

A simple regression method was also used on the Nebria results (Table 5.28 and Figure 5.24). This approach uses the ratio of marked to unmarked beetles to produce an estimate of the population size. It requires a more or less constant rate of change of ratio with time.

Table 5.25: Tabulation of recapture data according to the date on which the animal was last caught, for analysis by Jolly's method: Nebria brevicollis (following instructions in Southwood 1966, after Jolly 1965).

Date	Total Captured	Total Released	n_i	a_i	Day when last captured (j)
Sept 16	32	31	(1)	2	(1)
17	45	40	2	2	(2)
21	66	58	2	1	(3)
22	18	17	0	0	3 (4)
23	33	30	0	0	2 0 (5)
24	113	111	1	3	1 1 5 (6)
25	181	31	2	4	4 2 3 11 (7)
28	106	99	1	0	2 1 0 2 1 (8)
29	123	113	0	0	2 0 2 6 0 16 (9)
30	59	54	2	0	0 0 1 0 1 3 7 (10)
Oct 1	147	77	0	1	0 0 0 3 1 6 10 15 (11)
5	14	14	1	0	0 0 0 0 1 0 1 (12)
6	140	124	0	0	1 1 0 4 3 9 0 2 5 4 (13)
7	64		0	0	2 0 2 0 0 2 0 1 2 0 2 0 (14)
		R_i	9	17	5 11 28 7 35 20 17 8 4 0

Table 5.26: Calculated table of the total number of marked beetles recaptured on a given day (i) bearing marks of day (j) or earlier (following instructions in Southwood 1966, after Jolly 1965).

		Day i-1															
(1)	2	2	3	0	0	1	2	1	0	2	2	0	1	0	0	9	Z ₂
	(2)	3	0	0	4	6	10	3	0	2	2	1	1	0	15	29	Z ₃
	(3)	2	2	5	10	4	4	2	2	2	2	1	1	0	32	45	Z ₄
	(4)	2	2	6	12	4	4	2	2	2	2	1	1	0	34	56	Z ₅
	(5)	2	2	11	15	4	4	2	2	2	2	1	1	0	43	77	Z ₆
	(6)	2	2	11	26	7	10	4	4	4	2	2	2	0	49	118	Z ₇
	(7)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₈
	(8)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₉
	(9)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₀
	(10)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₁
	(11)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₂
	(12)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₃
	(13)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₄
	(14)	2	2	11	26	7	10	4	4	4	2	2	2	0	7	18	Z ₁₅

$$Z(i-1) + 1 = \begin{matrix} 9 & 15 & 29 & 32 & 32 & 34 & 34 & 43 & 49 & 30 & 34 & 9 & - \\ Z_2 & Z_3 & Z_4 & Z_5 & Z_6 & Z_7 & Z_8 & Z_9 & Z_{10} & Z_{11} & Z_{12} & Z_{13} & \end{matrix}$$

Table 5.27: The final table for a Jolly type mark and recapture analysis (after Jolly 1965).

Nebria brevicollis

Date	Day	i	Proportion of recaptures	$\hat{\alpha}_i$	Number of marked beetles at risk	\hat{M}_i	Total Population	\hat{P}_i	Survival rate	\hat{Q}_{c-i}	Number of new beetles	\hat{B}_{c-i}
Sept	16	1	-	-	0	0	-	-	0.778	0.778	-	-
	17	2	0.0444	0.0444	42	42	945.95	945.95	0.102	0.102	42	42
	21	3	0.0455	0.0455	8.12	8.12	178.47	178.47	1.609	1.609	8.12	8.12
	22	4	0.1667	0.1667	101.6	101.6	609.44	609.44	0.772	0.772	101.6	101.6
	23	5	0.0606	0.0606	89.27	89.27	1473.1	1473.1			89.27	89.27
	24	6	0.0973	0.0973	137.86	137.86	1416.9	1416.9			137.86	137.86
	25	7	0.1437	0.1437	176.57	176.57	1228.6	1228.6			176.57	176.57
	28	8	0.0660	0.0660	103.17	103.17	1563.2	1563.2			103.17	103.17
	29	9	0.2114	0.2114	268.95	268.95	1272.4	1272.4			268.95	268.95
	30	10	0.2373	0.2373	169.68	169.68	715.08	715.08			169.68	169.68
Oct	1	11	0.2449	0.2449	324.75	324.75	1326.0	1326.0			324.75	324.75
	5	12	0.2857	0.2857	123	123	430.53	430.53			123	123
	6	13	0.2071	0.2071	∞	∞						
	7	14	0.1406	0.1406	-	-						

Table 5.28: *Nebria brevicollis* Table of mark and release-recapture results for regression method of population estimation.

Date	Catch		Release New or Old Marks		Total Marks	Proportion unmarked in sub- quent catch
	Unmarked	Marked				
Sept						
14	40	-	40	-	40	100%
15	30	-	27	-	67	100%
16	32	-	31	-	98	93.3%
17	42	3	37	3	135	91.9%
20	91	8	77	7	212	86.2%
21	57	9	49	9	261	77.7%
22	14	4	13	4	274	93.8%
23	31	2	28	2	302	80.4%
24	91	22	89	22	391	81.2%
25	147	34	nil	31	391	81.8%
27	232	51	2	32	393	90.7%
28	96	10	90	9	483	74.9%
29	92	31	84	29	567	74.5%
30	44	15	39	15	606	70.1%
Oct						
1	103	44	34	43	640	74.2%

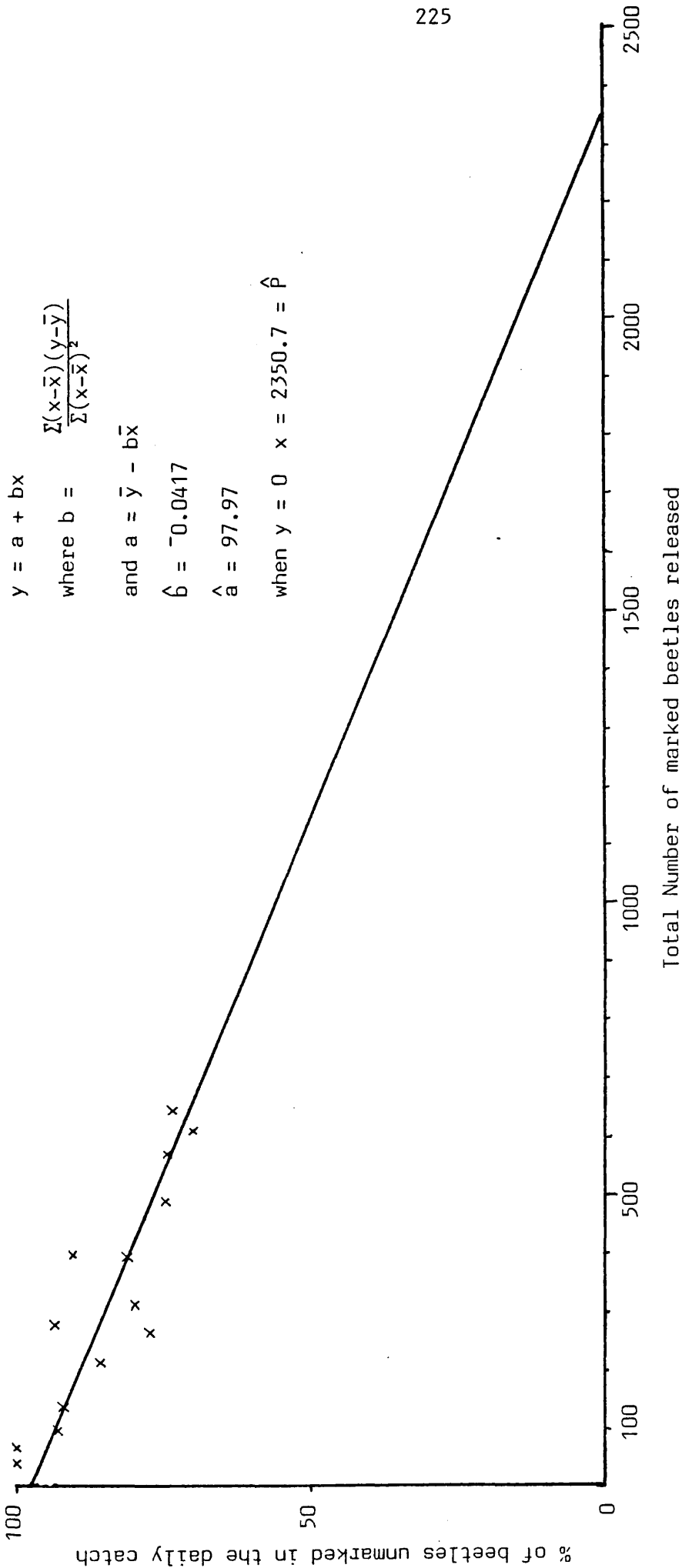


Figure 5.24 Nebria brevicollis : Population estimation by regression method from 16 Sept-1 October 1976.

Even if the population activity levels are changing, the ratio should be a good estimate of the true ratio within the population each day, as long as recruitment is at a steady low level, and the time period examined sufficiently short. It therefore has the advantage of being independent of daily activity changes, unlike the Jolly-Seber method.

The Nebria results produced a regression line crossing the x axis (total number of beetles) at 2350.7 (Figure 5.24). This may be compared with the Jolly-Seber estimate of 1563. The regression estimate is half as much again of the other method. However, both are substantially low densities of beetles.

It is interesting to note that the total number of beetles which are known to have been alive in the autumn of 1976 and within the study area at some time is around 1700 (all beetles captures between August 30th 1976 and May 6th 1977 - the latter date being before the appearance of any of the new generation). This figure will obviously include immigrant beetles but makes an interesting comparison with the two estimates of total beetles.

The other four species under consideration do not lend themselves to any method of population estimation since they exhibit very low recapture rates. In addition both Carabus violaceus and Pterostichus niger were present in relatively low numbers. During the period 20th July 1976 to 20th July, 1977, the total numbers of P. madidus caught and released marked were 561 females and 807 males (1368 total - a few beetles died in the traps). The total figure is not far short of the Nebria population size estimates. However, the low mobility and recapture rates of this species indicates the majority of the beetles of

this species are not being captured. (NB source of unmarked beetles within grid see 5.370). Thus the population size must be very much greater than that of Nebria - a figure approaching 1 per m² may not be unrealistic.

The total captures for the year 1976 of Abax parallelepipedus, Pterostichus niger, and Carabus violaceus were 471, 43 and 84 respectively. The recapture rates and low daily catches make the value of population estimation dubious.

Densities calculated by other authors for the species in woodland are as follows:

<u>Nebria brevicollis</u>	♂♂	0.39 m ⁻²	(Manga, 1972)
	♀♀	0.33 m ⁻²	(" ")
	both sexes	0.945-0.570 m ⁻²	(Penney, 1966)
" "		0.21 m ⁻²	(Haines, 1973)
" "		0.2 m ⁻²	(Tipton, 1960)
<u>Pterostichus madidus</u>	" "	10.8 m ⁻²	(Frank, 1967b)
	" "	0.57 m ⁻²	(1973:Kovalski, 1974)
	" "	0.43 m ⁻²	(1972: " ")
	" "	3.5 m ⁻²	(Mason, 1972)
	" "	1.4 m ⁻²	(" ")
<u>Abax parallelepipedus</u>	" "	5.8 m ⁻²	(Frank, 1967b)
	" "	1.8 m ⁻²	(Mason, 1972)
	" "	0.33 m ⁻²	(Haines, 1973)

5.400 Conclusions

- (i) recapture rates of the different sexes similar, with the exception of Abax where the rate was significantly higher in males.
- (ii) the distributions of the beetles within the study area are aggregated, especially in Nebria

- (iii) no change in the distribution with the onset of breeding activities could be detected in Nebria; Pterostichus madidus inconclusive
- (iv) the distribution of catches per trap is unimodal in all cases
- (v) multiple recaptures of Nebria brevicollis and female P. madidus were more frequent than would be expected
- (vi) greatest dispersal of Nebria occurs in autumn: peak in mid October, although peak activity in late September; dispersal level remains high in beetles in their second breeding season, whereas it falls off in the new generation beetles; no evidence of directional preference in dispersal found; a small proportion of the beetles disperse rapidly and soon leave the study area, although majority more static
- (vii) significant lack of displacement with time in P. madidus: all year round in females, but only outside the breeding season in males; second year males dispersal high June - Jly., but August in new generation; beetles of this species appear to be maintaining their locations in the study site
- (viii) low dispersal rates in Abax, although highest early in season
- (ix) results too few in Carabus violaceus and Pterostichus niger for useful comment
- (x) beetles tend to remain in the areas where they are in the highest densities
- (xi) new individuals are not only immigrants, but also beetles from within the study area which have avoided previous capture
- (xii) densities of Nebria 0.1 per m², and P. madidus probably up to 1 per m².

Chapter 6

Experimental Displacement of Individual Beetles

6.100 Introduction

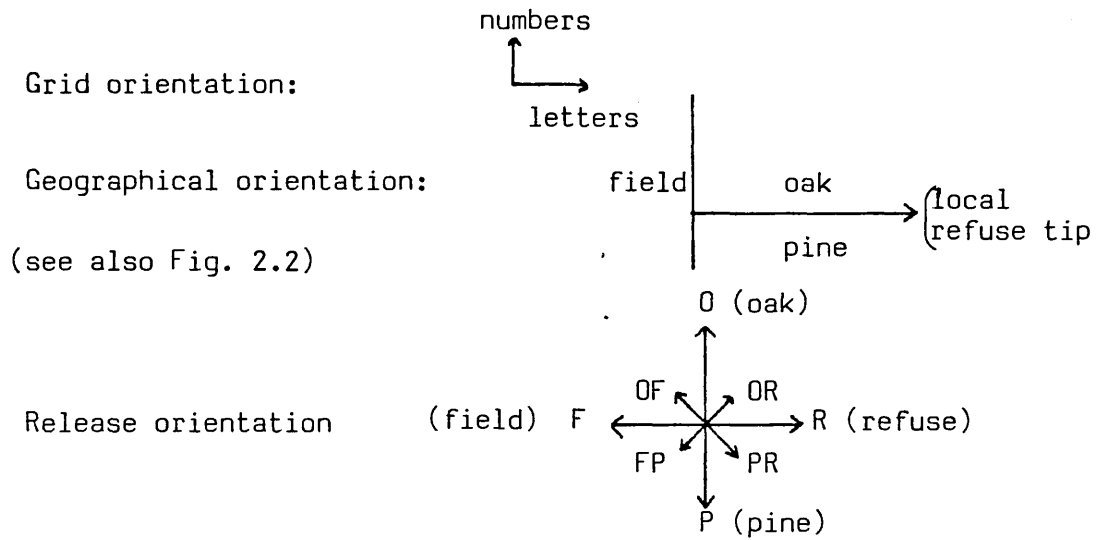
Following indications of possible home ranging behaviour in some species, the question of site attachment was investigated. The frequency distribution of multiple recaptures for Nebria brevicollis and female Pterostichus madidus showed more high frequencies than would be expected for independent capturing (5.340). In addition, a significant lack of displacement with time was exhibited by P. madidus beetles, particularly females (5.353).

In this section, therefore, captured beetles were not released by their trap of origin (as had been the case previously: Ch. 5), but at other, predetermined locations in the study site.

6.200 Methods

During the period May 12 - Nov. 3, 1977, traps at locations A-H, 1-10 were in use (80 traps, see Fig. 2.2), and from November 4, 1977 until April 20, 1978, A-H, 1-8 only (64 traps). Experimental procedures during these periods followed those described in Chapter 5, with the exception that the release points were varied as follows : for each day's catch, all the beetles were released at one particular distance from the trap of origin; distances used on different days were 1, 2, 4, 8, 12 and 15 metres; the direction of the release points was varied for each trap on a daily basis and corresponded to eight directions based on the grid axis (Figure 6.1).

Catch numbers during the above periods were low, with few recaptures. The effort was therefore concentrated to boost the results: the existing grid was closed down on the 20th April 1978, and replaced by another at locations P-X, 1-8 (64 traps at 5m intervals). This



direction varied daily for each trap in anticlockwise motion with traps out of phase with each other.

eg. on day 1	trap G5	beetles released at 2m distance in direction OF
	" A9	" " 2m " " P
day 2	" G5	" " 8m " " F
	" A9	" " 8m " " PR
day 3	" G5	" " 1m " " FP
	" A9	" " 1m " " R

Figure 6.1 Diagram to show derivation of release points.

particular section of the main grid was selected as one fairly uniform in vegetation and litter characteristics (see Figs 2.2 and 2.4), and also where P. madidus was most frequent (see Fig. 5.3). A "20m" release category was also added to the release distances used. Trapping proceeded until 29 June 1978, when the traps were all closed. Some trapping continued as part of the investigations into the traps themselves after this date (see Chapter 3).

6.300 Results

The detailed mark-release records are to be found in Appendix 6.1. The recapture results for both the large and reduced grids are presented separately (Appendices 6.2-6.10). These are compared with the numbers released in Tables 6.1 and 6.2 for the large (A,H;1,10 and A,H;1,8) and small (P,X;1,8) grids respectively. In these tables only the beetles recaptured within 30 days of their release are included to keep the figures in line with the practice adopted in Chapter 5. No Carabus violaceus were captured in 1978, and a single Nebria brevicollis was recaptured in spring 1977, and so these species/periods are omitted from their respective tables.

The recapture rates were compared by treating the tables as contingency tables and calculating χ^2 statistics. The resulting figures are brought together in Table 6.3 (details in Appendix 6.11). In some cases the numbers of recaptures were too few to make such analysis useful.

A significant difference in recapture rate across the range of displaced releases was only found with the female Pterostichus madidus beetles in the 1977 season ($0.05 > P > 0.02$). Here the recapture rate

Table 6.1: Recapture rates for the species trapped 1977/78 in
grid A,H;1,8(10)

(i) Nebria brevicollis : Sept - Oct 1977

Release distance	1m		2m		4m		8m		12m		15m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	8	-	19	14	44	13	20	4	15	7	43	10
Beetles not recaptured	5	2	16	8	34	19	20	12	23	8	38	23
Marked release	13	2	35	22	78	32	40	16	38	15	81	33

(ii) Pterostichus madidus : May - Nov 1977

Release distance	1m		2m		4m		8m		12m		15m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	5	15	6	3	-	2	1	1	1	4	6	1
Beetles not recaptured	105	142	78	63	40	67	43	59	66	41	42	54
Marked release	110	157	84	66	40	69	44	60	67	45	48	55

(iii) Abax parallelepipedus : 1977

Release distance	1m		2m		4m		8m		12m		15m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	3	-	2	-	-	-	1	1	-	-	-	1
Beetles not recaptured	37	24	39	16	12	10	12	6	20	7	15	14
Marked release	40	24	41	16	12	10	13	7	20	7	15	15

Table 6.1: (Continued)

(iv) Pterostichus niger : 1977

Release distance	1m		2m		4m		8m		12m		15m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	-	2	10	4	4	8	9	3	7	10	2	1
Beetles not recaptured	14	16	16	18	15	15	10	22	40	42	9	19
Marked release	14	18	26	22	19	23	19	25	47	52	11	20

(v) Carabus violaceus : 1977

Release distance	1m		2m		4m		8m		12m		15m	
	♂	♀	♀	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	1	-	2	-	2	2	-	-	-	1	-	2
Beetles not recaptured	1	13	2	3	1	4	2	6	1	3	3	3
Marked release	2	13	4	3	3	6	2	6	1	4	3	5

Table 6.2: Recapture rates for the species trapped 1978 in grid

PX, 18.

(i) Nebria brevicollis 21 Apr - 6 May, 1978 - before appearance of callows.

Release distance	1m		2m		4m		8m		12m		15m		20m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	2	2	2	-	-	-	-	-	-	1	1	-	-	-
Beetles not recaptured	1	1	6	2	-	1	-	1	1	1	1	-	-	3
Marked release	3	3	8	2	-	1	-	1	1	2	1	-	-	3

(ii) Nebria brevicollis 7 May - June 28, 1978 - predominantly callows

Release distance	1m		2m		4m		8m		12m		15m		20m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	2	-	1	-	2	3	1	-	-	1	-	-	-	-
Beetles not recaptured	8	9	14	4	12	4	4	7	12	9	7	4	2	-
Marked release	10	9	15	4	14	7	5	7	12	10	7	4	2	-

(iii) Pterostichus madidus 21 Apr - 28 June, 1978 - all over-wintered beetles.

Release distance	1m		2m		4m		8m		12m		15m		20m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	13	24	5	11	5	13	4	5	4	2	4	7	2	2
Beetles not recaptured	50	122	17	54	15	42	19	36	15	52	21	43	4	23
Marked release	63	146	22	65	20	55	23	41	19	54	25	50	6	25

Table 6.2 (Continued).

(iv) Abax parallelepipedus 21 Apr - 28 June, 1978.

Release distance	1m		2m		4m		8m		12m		15m		20m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	26	8	23	7	13	3	14	7	14	1	13	4	3	1
Beetles not recaptured	34	21	24	9	9	9	18	6	28	11	22	11	3	4
Marked release	60	29	47	16	22	12	32	13	42	12	35	15	6	5

(v) Pterostichus niger: 21 Apr - 28 June, 1978.

Release distance	1m		2m		4m		8m		12m		15m		20m	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Recaptures (30 days)	-	-	-	1	-	-	-	1	-	-	-	-	-	-
Beetles not recaptured	3	9	-	-	2	1	2	1	3	1	-	1	-	1
Marked release	3	9	-	1	2	1	2	2	3	1	-	1	-	1

Table 6.3: Results of comparison of recapture rate with distance from source of release point.

Species	Sex	Time period	Table	χ^2	Degrees of freedom	Probability
<u>Nebria brevicollis</u>	♂	Sept/Oct 1977	6.1i	3.639	5	0.70>P>0.50
"	♀	"	"	6.437	4	0.20>P>0.10
<u>Pterostichus madidus</u>	♂	May/Nov 1977	6.1ii	0.033	2	0.99>P>0.98
"	♀	"	"	6.414	2	0.05>P>0.02
"	♂	Apr/Jun 1978	6.2iii	0.468	5	P>0.99
"	♀	"	"	8.546	4	0.10>P>0.05
<u>Abax parallelepipedus</u>	♂	"	6.2iv	4.844	5	0.50>P>0.30
"	♀	"	"	0.788	3	0.90>P>0.80
<u>Pterostichus niger</u>	♂	1977	6.1v	7.361	3	0.10>P>0.05
"	♀	"	"	1.395	2	P≈0.50

fell with increasing distance from source trap - from 15/157 (c. 10%) at 1m, to 3/66 (c. 4.5%) at 2m and 1/55 (c. 1.8%) at 15m.

In addition to recapture rate, the rates of displacement of the individual beetles were examined. The distances achieved by each beetle between the release and recapture points were divided by the time interval (in days) and then these "dispersal rates" were regressed with the distance of the release point from the source trap (figures from Appendix 6.2). Thus any relationship between the rate of displacement by the individual beetles and the artificial displacement of the release point can be determined.

In Table 6.4 the recapture results for each release category have been grouped together to show the mean displacement rates of the beetles. The statistics generated by the regression analyses are displayed in Table 6.5. The regression coefficients were compared with the critical values of the 'F' distribution, and none were found to be significant. Thus displacement rate is not significantly related to the release point displacement.

Having examined recapture rate and displacement rate, the question of direction of movement remains. The approach to this was to separate the recapture results according to whether or not the recapture point was closer to the source trap than was the release point, i.e. examine the proportion moving closer to the source trap (Table 6.6). The individual tables were treated as contingency tables and a value of χ^2 calculated (where samples were sufficiently larger). Where a significant difference was found (Table 6.6, i, xiv, and xv), visual examination of the figures shows that the ratios in the first three

Table 6.4: Analysis of the effect of release distance on displacement rates of the beetles.

Species	Sampling period	Release category m.	Male beetles				Female beetles			
			Sample size (n)	Sum of displ. rates ($\sum \text{md}^{-1}$)	Mean rate (md^{-1})	Var (s^2)	n	$\sum \text{md}^{-1}$	md^{-1}	s^2
<u>Nebria brevicollis</u>	Sept-Nov 1977	1	4	18.05	4.51	58.85	nil	-	-	-
		2	9	21.22	2.36	8.70	7	15.0	2.14	4.33
		4	20	118.20	5.91	75.86	5	8.17	1.63	0.32
		8	13	51.18	3.94	7.67	2	5.9	2.95	13.03
		12	15	74.45	4.96	30.57	5	44.57	8.91	184.96
		15	23	311.64	13.55	189.58	8	36.13	4.52	16.08
<u>Pterostichus niger</u>	1977	1	nil	-	-	-	2	6.7	3.35	2.65
		2	8	28.50	3.56	4.70	3	3.97	1.32	0.73
		4	3	5.57	1.86	2.20	5	21.94	4.39	57.94
		8	1	1.4	1.4	-	1	3.0	3.0	-
		12	5	21.36	4.34	20.02	6	53.50	8.92	137.98
		15	1	1.71	1.71	-	1	4.25	4.25	-
<u>Carabus violaceus</u>	1977	1	1	4.14	4.14	-	nil	-	-	-
		2	2	6.86	3.43	-	nil	-	-	-
		4	2	8.28	4.14	-	2	11.6	5.8	-
		8	nil	-	-	-	nil	-	-	-
		12	nil	-	-	-	1	2.25	2.25	-
		15	nil	-	-	-	2	7.89	3.95	-

Continued

Table 6.4: (Continued)

Species	Sampling period	Release category m.	Male beetles			Female beetles				
			Sample size (n)	Sum of displ. rates (Σmd^{-1})	Mean rate (md^{-1}) (s^2)	Var (s^2)	n	Σmd^{-1}	md^{-1}	s^2
<u>Nebria brevicollis</u>	Apr-June 1978	1	3	4.99	1.67	5.41	2	8.96	4.48	0.04
		2	2	9.67	4.83	34.72	nil	-	-	-
		4	2	7.17	3.58	3.99	2	3	1.5	0.5
		8	1	1.6	1.6	-	nil	-	-	-
		12	nil	-	-	-	1	2.11	2.11	-
		15	1	0.91	0.91	-	nil	-	-	-
<u>Pterostichus madidus</u>	Apr-June 1978	1	8	19.94	2.49	5.80	23	37.01	1.61	3.64
		2	1	0.67	0.67	-	8	11.57	1.45	0.13
		4	3	3.84	1.28	0.40	11	7.97	0.72	0.43
		8	1	0.14	0.14	-	4	4.05	1.01	0.72
		12	2	3.3	1.65	0.25	1	12	12	-
		15	3	11.2	3.73	12.63	6	11.71	1.95	5.64
		20	1	2.0	2.0	-	1	0.55	0.55	-
		20	17	62.90	3.70	22.43	8	6.75	0.84	0.40
<u>Abax parallelepipedus</u>	Apr-June 1978	2	15	28.55	1.90	1.37	6	9.13	1.52	1.78
		4	11	23.04	2.09	3.73	2	2.42	1.21	0.84
		8	11	32.57	2.96	12.22	6	10.53	1.75	2.76
		12	11	32.51	2.95	13.16	1	0.42	0.42	-
		15	11	20.59	1.87	2.90	3	3.76	1.25	2.29
		20	2	2.77	1.38	0.16	nil	-	-	-

Table 6.5: Results of regression analysis of recapture figures following displaced release.

Species and sampling period	Sex	SSR	Error Var.	Slope	St. error of slope	St. error of Y	Inter- cept	Varia- nce ratio	R ²	R	n	P
<u>Nebria brevicollis</u> Sept-Nov 1977	♂	6972.26	85.03	0.6165	0.1982	1.0061	1.7152	9.6798	0.1056	0.3249	86	>0.50
	♀	990.25	39.61	0.3157	0.223	1.2112	1.3762	2.005	0.0742	0.2725	28	>0.50
<u>Pterostichus niger</u> 1977	♂	134.68	8.42	0.0284	0.1443	0.6838	3.0768	0.0386	0.0024	0.0491	18	>0.75
	♀	976.84	61.05	0.4777	0.3875	1.8417	1.9221	1.5196	0.0867	0.2945	18	>0.75
<u>Carabus violaceus</u> 1977	♂	4.6285	1.5428	0.1175	0.4629	0.5555	3.55	0.0645	0.021	0.145	5	>0.75
	♀	64.908	21.636	-0.2035	0.4144	2.0802	6.3831	0.2411	0.0744	0.2727	5	>0.75
<u>Nebria brevicollis</u> Apr-June 1978	♂	65.356	9.3366	-0.1874	0.2333	1.0185	3.4046	0.6452	0.0844	0.2905	9	>0.75
	♀	7.0322	2.3441	-0.1923	0.1699	0.6847	3.6599	1.2808	0.2992	0.547	5	>0.50
<u>Pterostichus madidus</u> Apr-June 1978	♂	83.3287	4.9017	0.0377	0.0813	0.5079	1.9268	0.2154	0.0125	0.1119	19	>0.75
	♀	232.1938	4.4653	0.0632	0.0577	0.2876	1.279	1.2003	0.0226	0.1502	56	>0.75
<u>Abax parallelepipedus</u> Apr-June 1978	♂	837.339	8.0513	-0.0059	0.0497	0.2756	2.4586	0.0143	0.0001	0.0117	109	>0.75
	♀	36.5367	1.2599	0.0077	0.0373	0.2016	1.2436	0.0425	0.0015	0.0383	32	>0.75

Table 6.6: Comparison of direction of movement with release displacement

(i) Nebria brevicollis ♂♂ 1977/78 trapping period

Displacement on release (m)	1	2	4	8	12	15	Total
Nearer to source trap	5	13	20	7	7	11	63
No nearer	6	8	27	14	19	34	108
Total Recaptures	11	21	47	21	26	45	171

$\chi^2 = 11.076$
5 degrees of freedom
 $p \approx 0.05$

(ii) N. brevicollis ♀♀ 1977/78 trapping period

Displacement on release	1	2	4	8	12	15	Total
Nearer to source trap	(2 + 4 + 2)			(3 + 2)		(-)	13
No nearer	(-)	10	(+11)	(3 + 7 + 12)			43
Total recaptures	(2 + 14 + 13)			(6 + 9 + 12)			56

$\chi^2 = 0.645$
1 degree of freedom
 $0.50 > P > 0.30$

(iii) Pterostichus madidus ♂♂ May - June 1977

Displacement on release	1	2	4	8	12	15	Total
Nearer to source trap	1	4	-	-	-	-	5
No nearer	1	-	-	-	-	-	1
Total recaptures	2	4	-	-	-	-	6

(iv) P. madidus ♀♀ May - June 1977

Displacement on release	1	2	4	8	12	15	Total
Nearer to source trap	9	1	3	-	-	-	13
No nearer	-	-	-	1	-	-	1
Total recaptures	9	1	3	1	-	-	14

(v) P. madidus ♂♂ July - August 1977

Displacement on release	1	2	4	8	12	15	Total
Nearer to source trap	-	-	-	-	-	1	1
No nearer	6	3	-	1	1	4	15
Total recaptures	6	3	-	1	1	5	16

Continued

Table 6.6: (Continued)

(vi) P. madidus ♀♀ Jly - Aug 1977

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	-	-	-	2	-	-	2
No nearer	-	-	-	-	-	-	-
Total recaptures	-	-	-	2	-	-	-

(vii) P. madidus ♂♂ Sept - Nov 1977

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	-	-	-	-	-	1	1
No nearer	-	-	-	-	-	1	1
Total recaptures	-	-	-	-	-	2	2

(viii) P. madidus ♀♀ Sept - Nov 1977

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	5	2	-	-	2	-	9
No nearer	1	1	1	1	2	1	7
Total recaptures	6	3	1	1	4	1	16

Continued

Table 6.6: (Continued)

(ix) Pterostichus niger ♂♂ 1977

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	-	1	2	1	2	-	6
No nearer	-	9	2	8	5	2	26
Total recaptures	-	10	4	9	7	2	32

(x) P. niger ♀♀ 1977

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	-	2	-	-	1	-	3
No nearer	2	2	8	3	9	1	25
Total recaptures	2	4	8	3	10	1	28

(xi) Nebria brevicollis ♂♂ Apr - June 1978

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	1	1	-	1	-	1	4
No nearer	3	2	2	-	-	-	7
Total recaptures	4	3	2	1	-	1	11

(xii) N. brevicollis ♀♀ Apr - June 1978

Displacement of release	1	2	4	8	12	15	Total
Nearer to Source trap	-	-	1	-	1	-	2
No nearer	2	-	2	-	1	-	5
Total recaptures	2	-	3	-	2	-	7

Continued

Table 6.6: (Continued)

(xiii) P. madidus ♂♂ Apr - June 1978

Displacement at release	1	2	4	8	12	15	20	Total
Nearer to Source trap	1	1	-	3	1	-	-	6
No nearer	12	4	5	1	3	4	2	31
Total recaptures	13	5	5	4	4	4	2	37

(xiv) P. madidus ♀♀ Apr - June 1978 $\chi^2 = 7.679$ 2 degrees of freedom
0.05 > P > 0.02

Displacement at release	(1 / 2)	(4 / 8)	(12 / 15 / 20)	Total
Nearer to Source trap	(5 + 2)	(2 + 3)	(1 + 5 + 1)	19
No nearer	(19 + 9)	(11 + 2)	(1 + 2 + 1)	45
Total recaptures	(24 + 11)	(13 + 5)	(2 + 7 + 2)	64

(xv) Abax parallelepipedus ♂♂ Apr - June 1978 $\chi^2 = 21.452$ 2 degrees of freedom
P < 0.001

Displacement at release	(1 / 2 / 4 / 8)	12	(15 / 20)	Total
Nearer to Source trap	(1 + 1 + 1 + 5)	8	(4 + 1)	21
No nearer	(25 + 22 + 12 + 9)	6	(9 + 2)	85
Total recaptures	(26 + 23 + 13 + 14)	14	(13 + 3)	106

(xvi) A. parallelepipedus ♀♀ Apr - June 1978

Displacement at release	1	2	4	8	12	15	20	Total
Nearer to Source trap	1	1	-	2	-	3	-	7
No nearer	7	6	3	5	1	1	1	24
Total recaptures	8	7	3	7	1	4	1	31

columns (1, 2 and 4m) differ noticeably with those of the following columns (8, 12, 15 and 20m) in each case. However, in the first case (Nebria brevicollis ♂♂ (i)) the proportion of beetles recaptured closer to the source trap falls, but increases in the other two (Pterostichus madidus ♀♀ (xiv), and Abax parallelepipedus ♂♂ (xv)). The 4:8m effect is most likely due to the physical nature of the grid rather than some behavioural response in the beetles. In the last two cases the pitfall traps are spaced 5m intervals, and so displacements greater than this distance have traps close to them in the direction of the source trap whereas the reverse situation is true for lower displacements. Thus a beetle released at 4m distance is more likely to be caught in a trap in the opposite direction to the source trap than is one released at 8m distance, and vice versa. Thus geometrical difficulties obscure the results. It is perhaps more important to note that, generally speaking, the majority of beetles move away from the source trap. This is more evident with the 5m interval grid, where the chances of recapture in another trap are greater than in a 15m grid.

The numbers of beetles which are recaptured in the trap from which they were obtained are interesting in themselves. Many beetles displaced 15 metres are next captured in the source trap (Table 6.7 and 6.8). This is most evident with Nebria brevicollis - a species which has already been shown to be the most active of the five species being investigated (see Chapter 5), and which commonly covers greater distances in short time intervals. It is not surprising then that many are recaptured in the trap at which they were last found.

Table 6.7: Frequency of beetles recaptured in trap of previous capture
with varying release distance : 15m grid 1977/78.

(i) Nebria brevicollis ♂♂

♀♀

	♂♂							♀♀						
	1	2	4	8	12	15	Total	1	2	4	8	12	15	Total
Source trap	5	13	20	7	7	11	63	2	4	2	3	2	-	13
Other	6	8	27	14	19	34	108	-	10	11	3	7	12	43
Total	11	21	47	21	26	45	171	2	14	13	6	9	12	56

(ii) Pterostichus madidus

♂♂

♀♀

	♂♂							♀♀						
	1	2	4	8	12	15	Total	1	2	4	8	12	15	Total
Source trap	1	4	-	-	-	2	7	14	3	2	-	2	-	21
Other	4	2	-	1	1	5	13	1	1	1	1	2	1	7
Total	5	6	-	1	1	7	20	15	4	3	1	4	1	28

(iii) Abax parallelepipedus

♂♂

♀♀

	♂♂							♀♀						
	1	2	4	8	12	15	Total	1	2	4	8	12	15	Total
Source trap	3	2	-	-	-	-	5	-	-	-	1	-	-	1
Other	-	-	-	1	-	-	1	-	-	-	-	-	1	1
Total	3	2	-	1	-	-	6	-	-	-	1	-	1	2

(iv) Pterostichus niger

♂♂

♀♀

	♂♂							♀♀						
	1	2	4	8	12	15	Total	1	2	4	8	12	15	Total
Source trap	-	1	2	1	2	-	6	-	2	-	-	1	-	3
Other	-	9	2	8	5	2	26	2	2	8	3	9	1	25
Total	-	10	4	9	7	2	32	2	4	8	3	10	1	28

Continued

Table 6.7: (Continued)

(v) Carabus violaceus

♂♂

♀♀

	♂♂							♀♀						
	1	2	4	8	12	15	Total	1	2	4	8	12	15	Total
Source trap	-	1	1	-	-	-	2	-	-	1	-	-	-	1
Other	1	1	1	-	-	-	3	-	-	1	-	1	2	4
Total	1	2	2	-	-	-	5	-	-	2	-	1	2	5

Table 6.8: Location of subsequent capture following displaced release;

5m grid April - June 1978.

(i) Pterostichus madidus ♂♂

Release distance	1	2	4	8	12	15	20	Total
Source Trap	1	1	-	-	-	-	-	2
Other	12	4	5	4	4	4	2	35
Total recaptures	13	5	5	4	4	4	2	37

(ii) P. madidus ♀♀

Release distance	1	2	4	8	12	15	20	Total
Source Trap	5	2	2	-	-	-	-	9
Other	19	9	11	5	2	7	2	55
Total recaptures	24	11	13	5	2	7	2	64

(iii) Abax parallelepipedus ♂♂

Release distance	1	2	4	8	12	15	20	Total
Source Trap	1	1	1	1	2	-	1	7
Other	25	22	12	13	12	13	2	99
Total recaptures	26	23	13	14	14	13	3	106

(iv) A. parallelepipedus ♀♀

Release distance	1	2	4	8	12	15	20	Total
Source Trap	1	1	-	-	-	-	-	2
Other	7	6	3	7	1	4	1	29
Total recaptures	8	7	3	7	1	4	1	31

6.400 Discussion

The basic premise behind the experiments described in this chapter is that an animal exhibiting site attachment, or a static home range, will react differently to an unfamiliar location as compared with its home location. Therefore, by releasing a captured beetle some distance from the capture point, and retrapping at a later date, behavioural changes may be sought. By varying these distances it was hoped to discover the boundaries between "familiar" and "unfamiliar" locations, if such distinctions exist to the beetles.

The recapture rate was not found to vary with the release displacement, with one exception. Thus displacement does not result in an increased loss of experimental animals, either through mortality or emigration. This indicates that relocation within suitable habitat has no adverse effects on the beetles. The exception was female Pterostichus madidus beetles in the 1977 trapping season. However, this was not repeated in 1978 when a greater concentration of traps was in use. The decreased rate therefore appears to be the result of the low dispersal rate already observed in this species elsewhere (see Chapter 6).

The calculated dispersal rates did not change significantly with increasing release displacement. Therefore, the beetles exhibited no disturbance activity following relocation. It is interesting to note that the 5m trap interval resulted in many displacements of female P. madidus, where they were rare with 15m trap intervals. The recapture rate was also much higher with the smaller grid - the males recapture rate doubled (151/1488, i.e. 10.2% in 1976 [Table 5.12] and 37/178, i.e. 20.8% in 1978 [Table 6.2iii]), and female rate increased

by nearly a third (99/885, i.e. 11.2% in 1976, and 64/436, i.e. 14.7%, in 1978). The two sets of figures refer to different time periods and grid areas, but this is unlikely to have produced the effect alone. This is further evidence that the recapture characteristics of this species are the result of low dispersal rates, rather than localised home ranging.

Some directional effects between release and recapture locations were found, but the geometry of the grid is probably the main cause of this: the effect being strongest at the point where geometrical considerations indicate the greatest change in recapture potential. The lack of a general trend of movement towards the areas from which the beetles were displaced indicates little awareness of location within the study area.

The overall conclusion that the beetles do not restrict their activities to areas of familiar ground has bearing on the discussion of methods (Chapter 3). It was pointed out that release points should be carefully considered, and judgements based on knowledge of the spatial behaviour of the species being used. This information has now been produced and, interestingly, justifies the techniques of authors who have ignored the question.

6.500 Conclusion

No evidence was found to support the idea of a static home range in any of the species studied.

Chapter 7

Mobility at the Individual Level

7.100 Introduction

In the preceding chapters release-recapture results have largely been treated as single, unrelated events. However, in many cases, a number of these events refer to the same individual beetle. Each movement should not be assumed as independent of all previous movements. It is important that the relationships between subsequent displacements are examined in a single individual, if only to illustrate the general conclusions derived from the pooled results.

The role of individual variation in population stability and emigration has been stressed recently (Lomnicki, 1978) and it seems appropriate at this stage in the study to examine that role in ground beetles (see also Chapter 3).

In this chapter the results are separated into three groups: (i) individuals captured on many occasions, (ii) individuals known to have been active in more than one breeding season, and (iii) those which were encountered in the study area actually in daytime refuges rather than pitfall traps. This last group consists of very few individuals as, generally, disturbance of the study area was kept to a minimum. Additionally, in Nebria brevicollis, some marked females, which died in the traps following overnight flooding due to rainfall, were dissected, and these results are presented here.

7.200 Nebria brevicollis

7.210 Multiple recaptures

A total of 41 individuals of this species were captured on six or more occasions during the trapping periods (1975-78). Of these 24 were definitely male, but only three female. The remaining 14

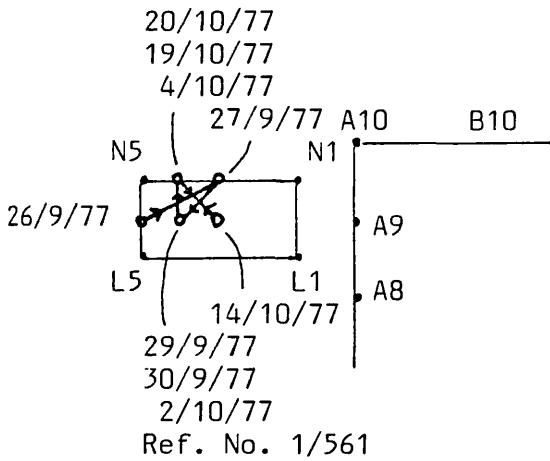
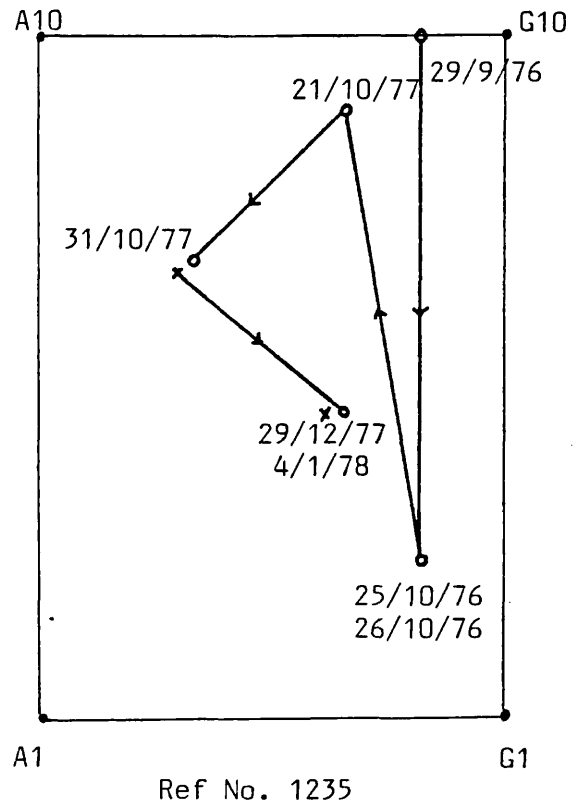
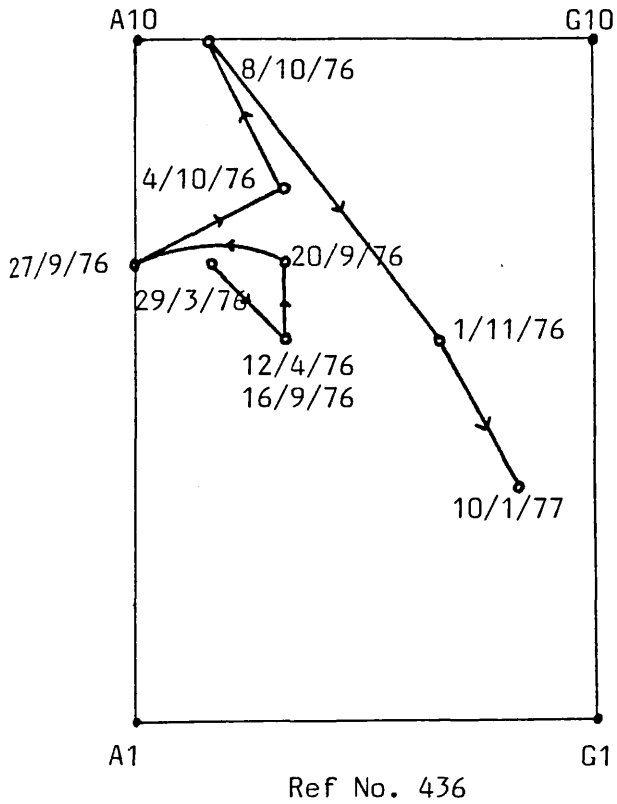
were the result of captures during the early stages of the study when the sexes were not separated.

Recapture frequency distributions are discussed elsewhere (Chapter 5.340).

The difference between the sexes is very significant ($P < 0.001$). A trend in favour of males would be expected since they exhibit greater nett displacement rates than the females (see Table 6.4) - an animal travelling further is more likely to encounter a trap. Details of the recaptures are given in Appendix 7.1 and a selection shown diagrammatically in Figures 7.1(i) to 7.1(ii). This selection was made on the basis of highest recapture frequency. Each of these beetles were found on the edge of the grid at some date and travel long distances within the grid. It is immediately obvious that the grid is too small to cover the range of these beetles.

Many of the time intervals between successive captures are too long for correlation with the detailed conclusions on activity and displacement made in 5.352. However, the exceptions to this do correlate rather well:

- (i) low activity and displacement in the spring visible in beetles 436 and 1/629,
- (ii) high activity, low displacement in early autumn in beetles 1/564 and 1/629,
- (iii) high activity, high displacement in mid autumn in beetles 436, 1235, 320, 798, 980, 1422, 1828 and 1/629
- (iv) lower activity, lower displacement late autumn in beetles 980 and 1828,
- (v) activity and displacement not falling off with older beetles, in 107, 233, 278, 465, 1/269, 436 and 1235.



Scale: 1cm represents 15m
 o : capture points
 x : release points where more than 1m from o

Fig. 7.1 (i) Nebria brevicollis: movements of female beetles

[NB. solid lines refer to shortest distance between two subsequent capture points,
 dotted lines refer to experimental displacement release points,
 throughout the diagrams in this chapter]

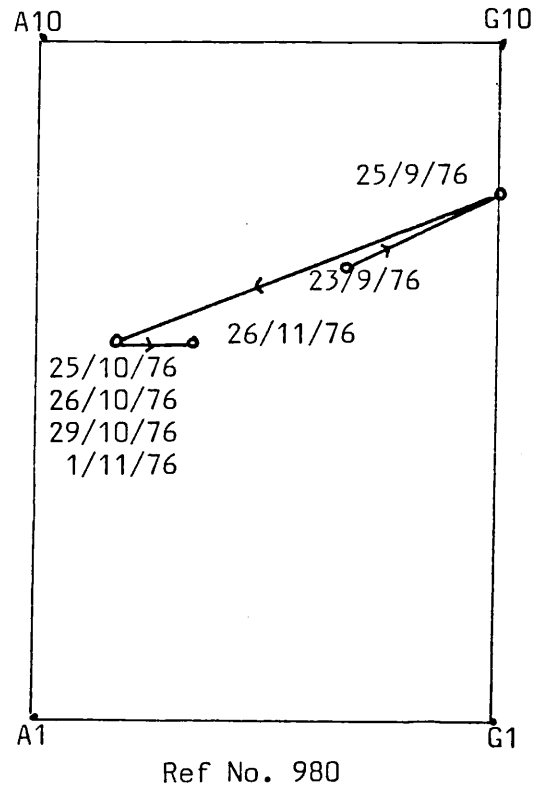
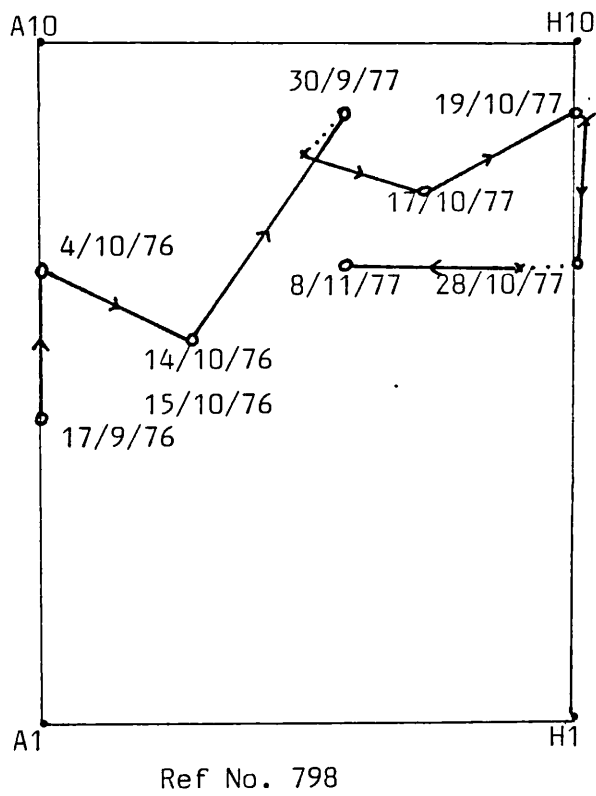
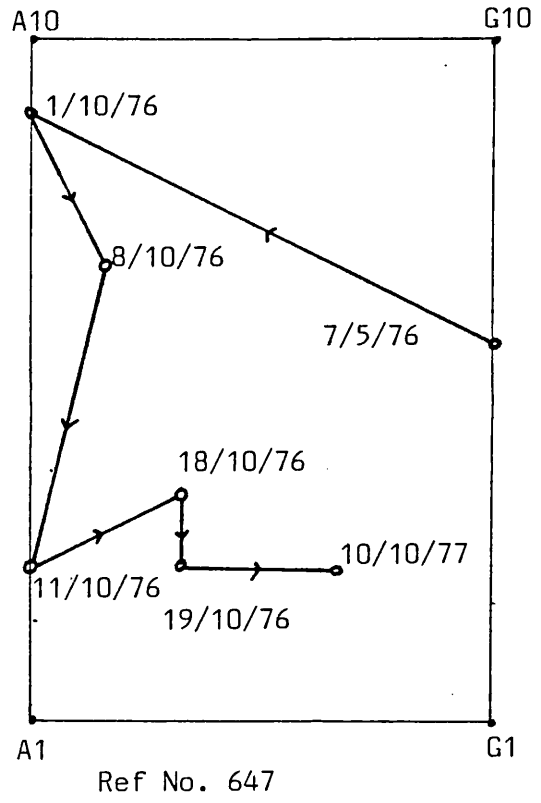
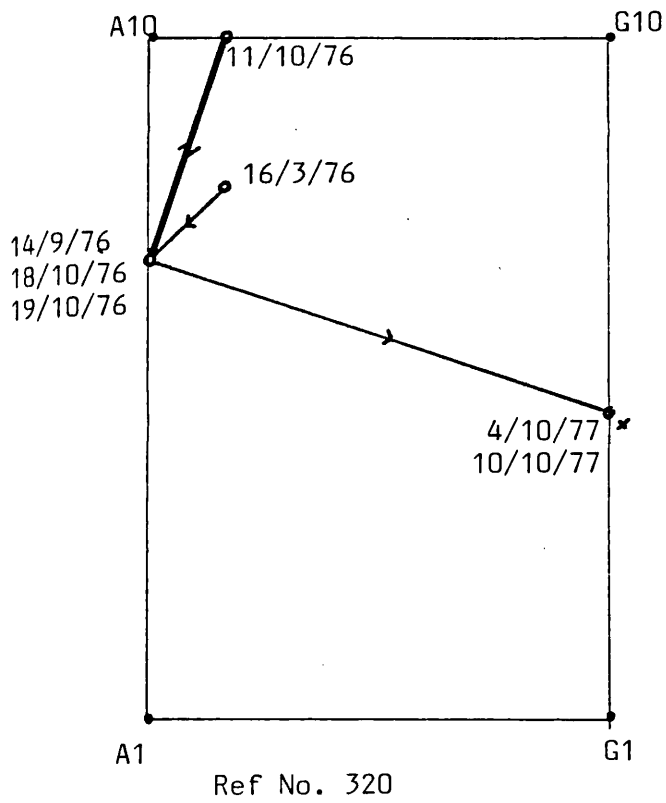
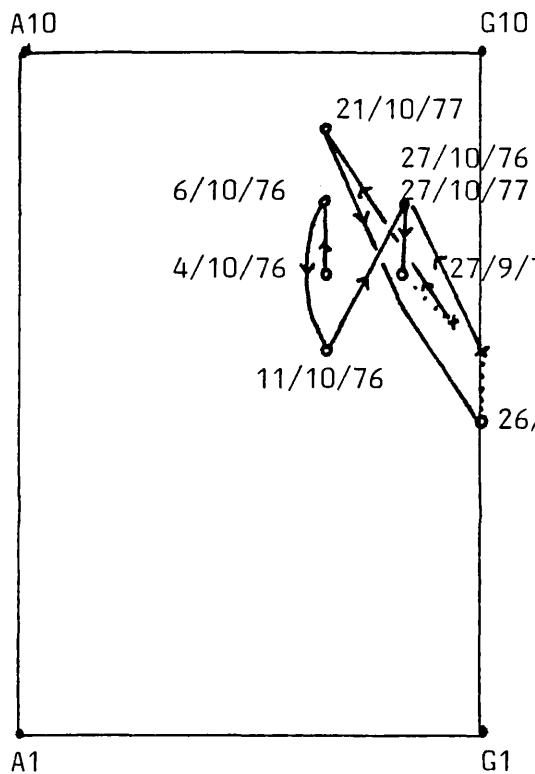
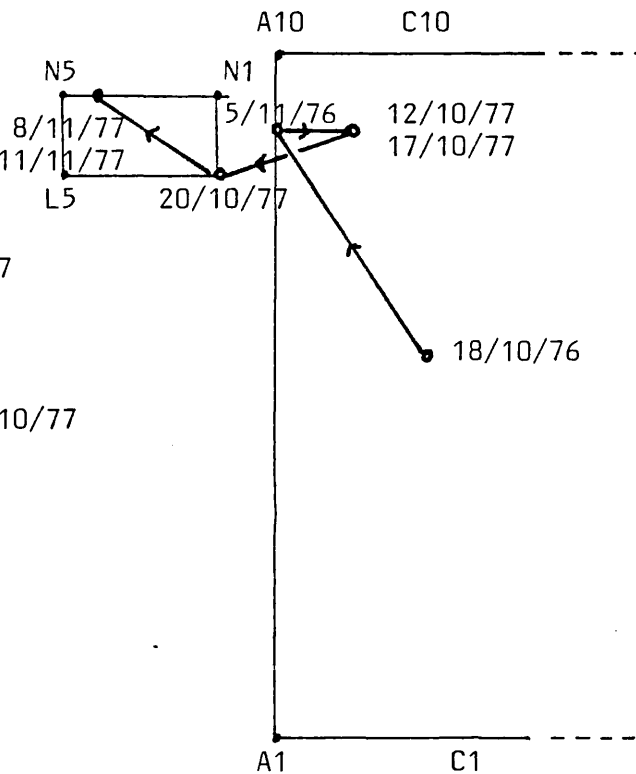


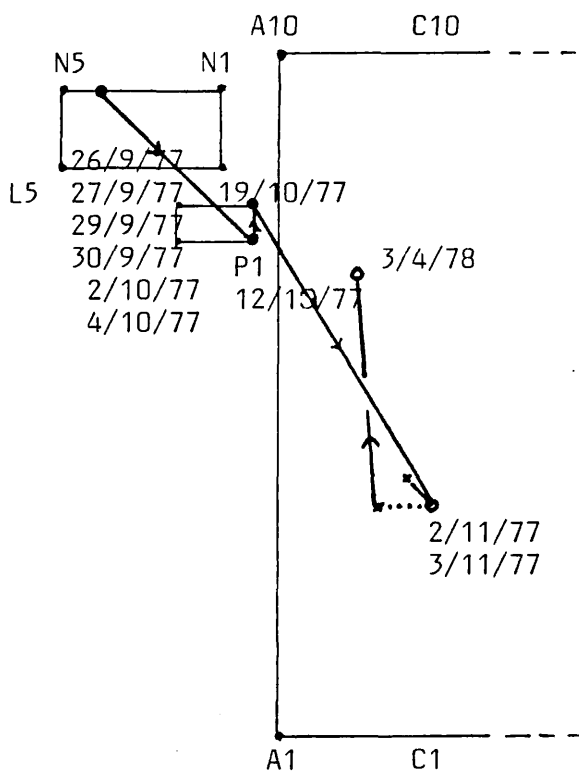
Fig. 7.1 (ii) Nebria brevicollis (female) continued.



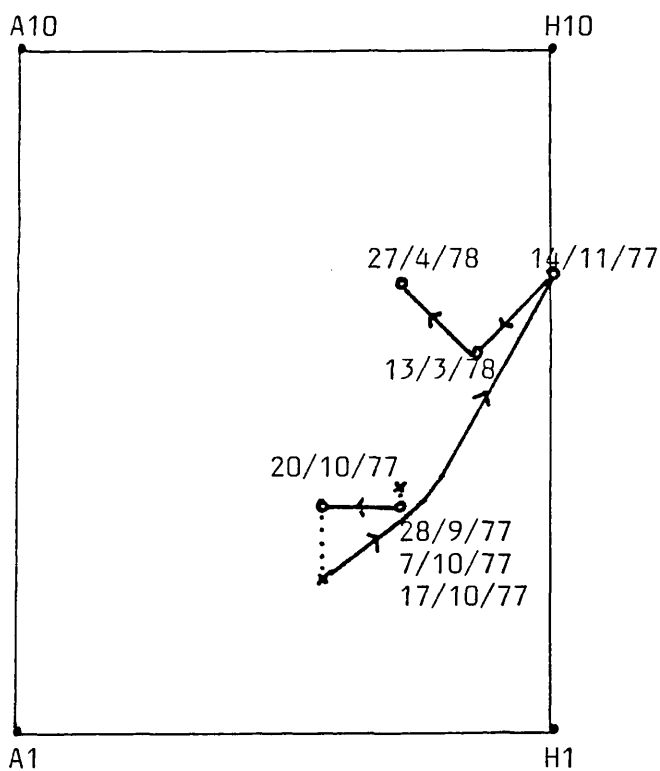
Ref No. 1422



Ref No. 1828



Ref No. 1/564



Ref No. 1/629

Scale: 1cm
represents 15m

Figure 7.1 (ii) Nebria brevicollis: movements of male beetles

7.220 Long-lived individuals

In this category are 18 male and 2 female beetles known to have been active beyond two breeding seasons : 9 males and one female which were active in the 1975 breeding season and were captured in 1977, some during that (their third) breeding season; and the same numbers and proportion of beetles active in the 1976 breeding season and present in 1978 (see Appendix 7.2). It is possible that some of these animals may also have been active as adults in the year preceding that in which they were first captured.

It is not surprising that some of these long-lived beetles are also the source of many multiple recaptures described in 7.210. Indeed, both females and two males were selected for illustration in that section (320, 436, 647 and 1235) and should be referred back to. The recapture histories of the other beetles are illustrated in Figure 7.2.

In view of the high activity and displacement levels of this species, it is likely that many of the individuals in this section have left the trapping areas and returned at a later date - six of those illustrated were taken in pitfall traps outside the main trapping grid; and specimens such as 1416 and 1942 are unlikely to have been active over such small ranges for more than a year. However, it is here that multiple recapture results come into their own. Specimen 233 was caught on six occasions over a period of about a year: the net displacement achieved was 60m and all intervening captures are between these two in space as well as time; only the first capture point was on the edge of the grid, and all the rest in the centre. Specimens 558, 278 and 1416 also show activity ranges within

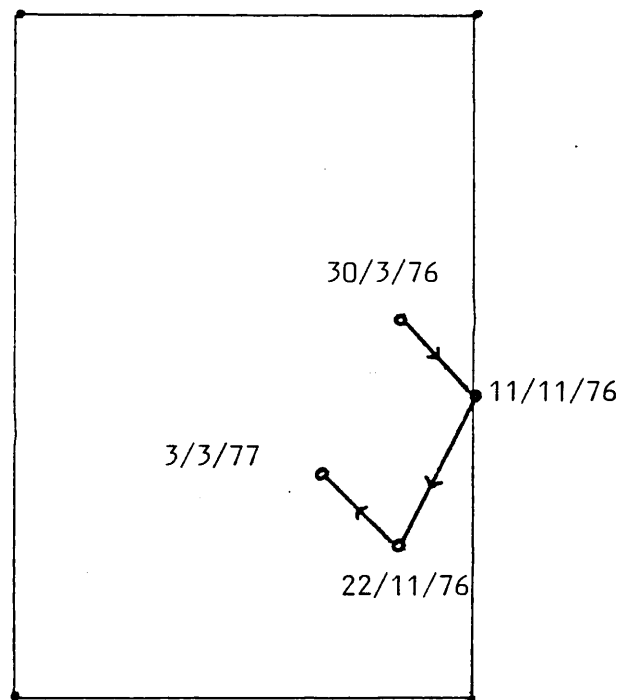
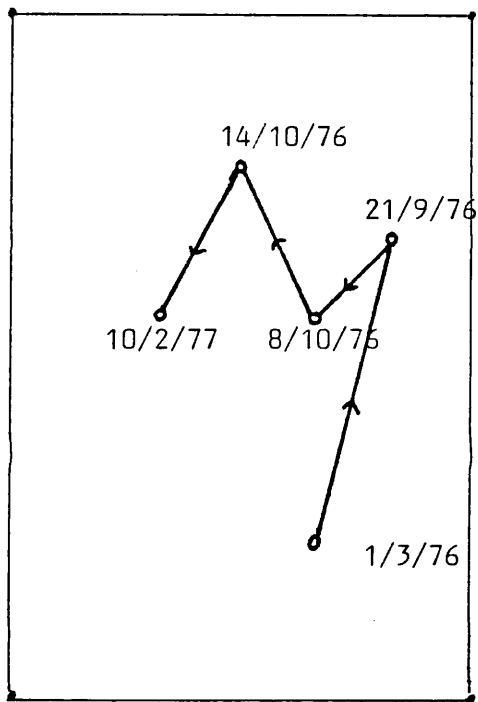
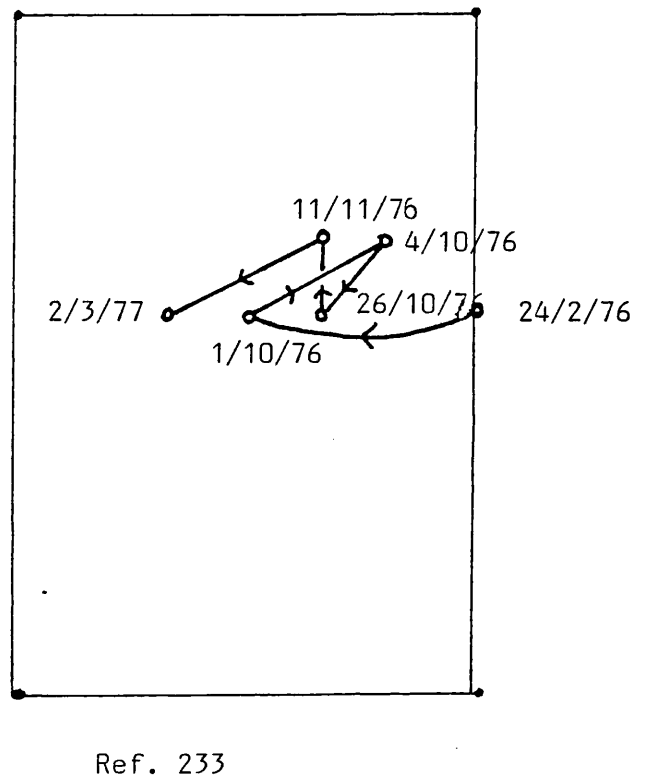
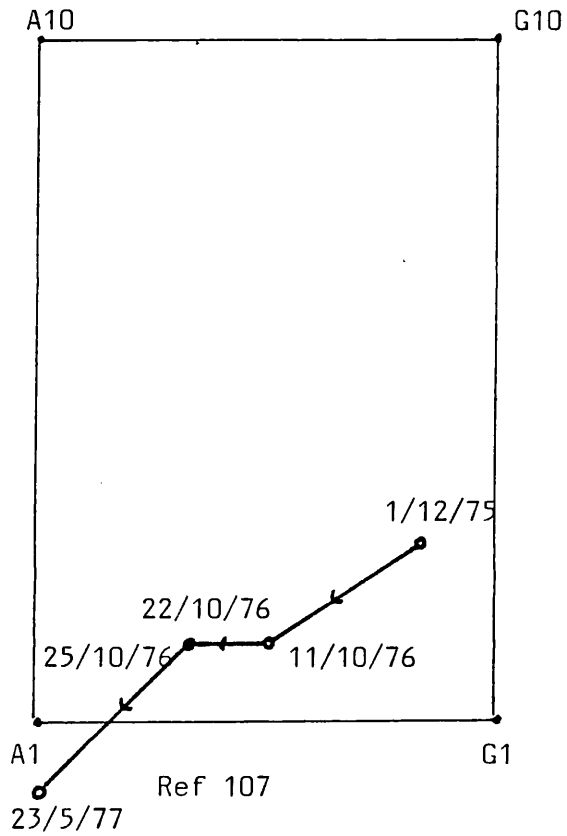


Figure 7.2 (i) Nebria brevicollis: movements of male beetles with long recorded histories (Scale 1cm represents 15m.).

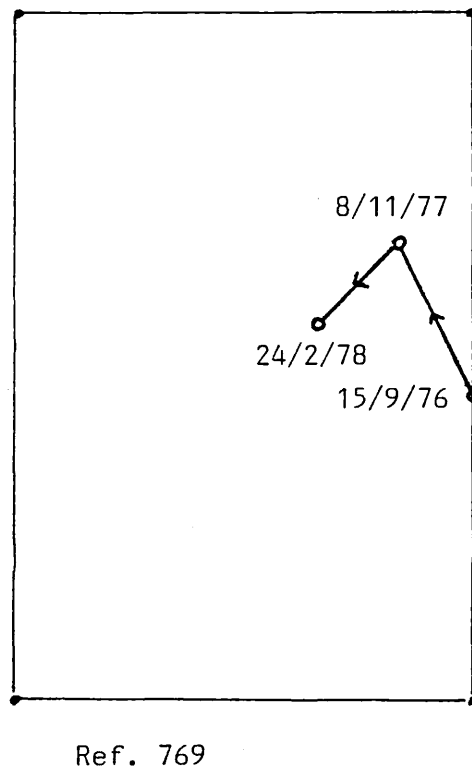
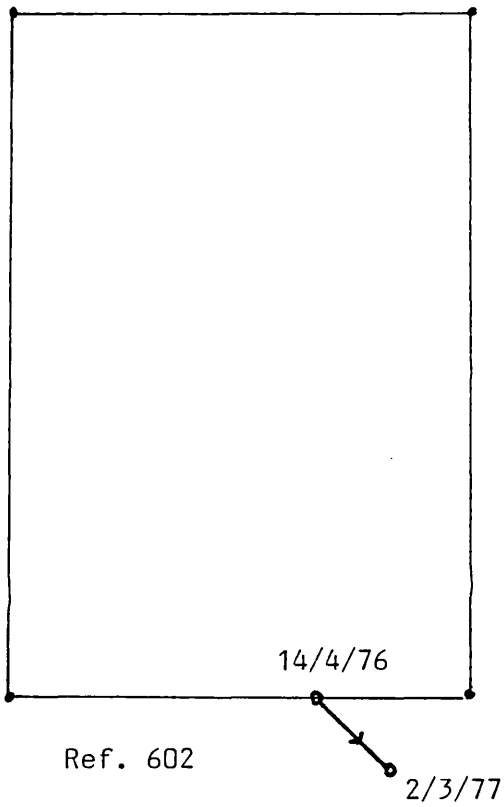
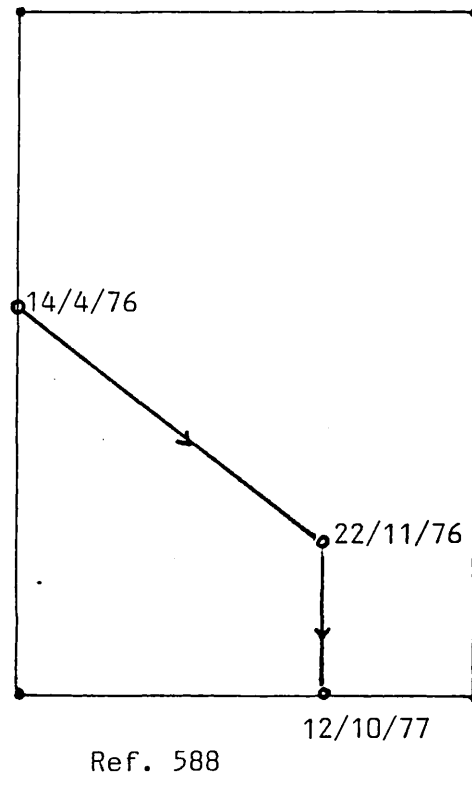
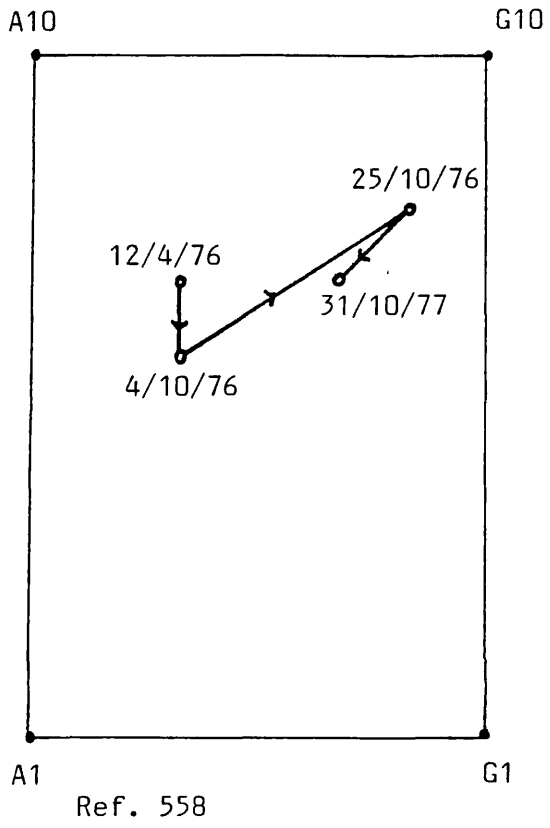
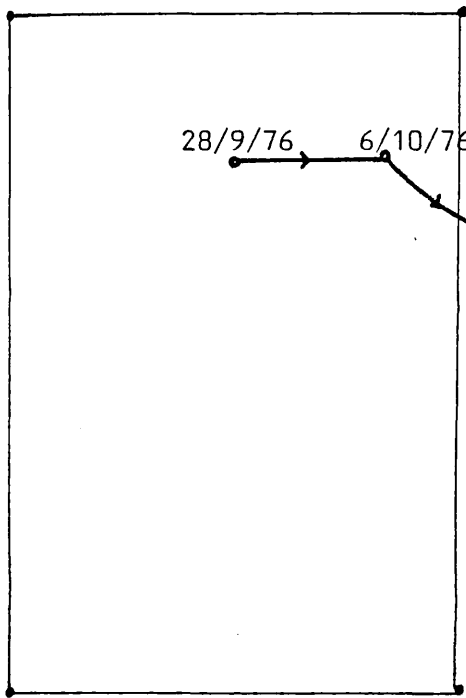
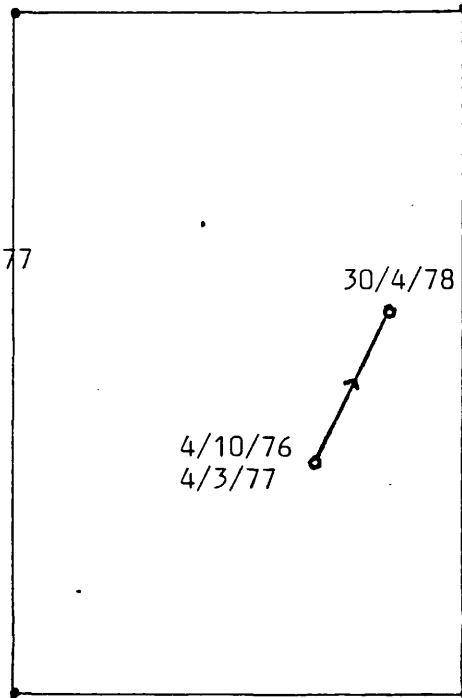


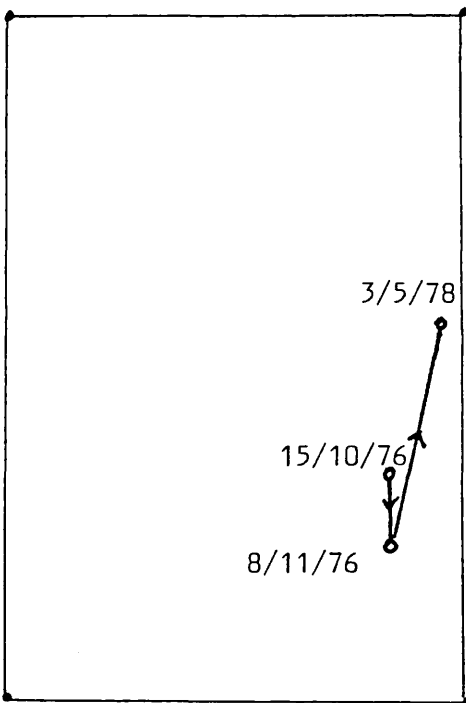
Figure 7.2 (ii) : Nebria brevicollis (male), continued



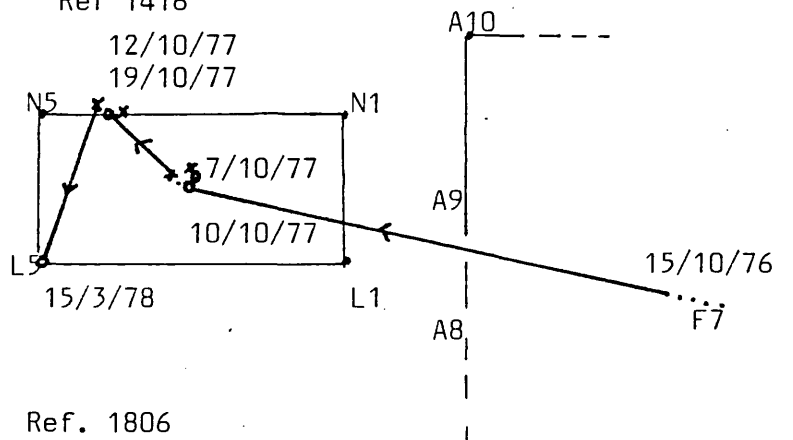
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Ref 1416



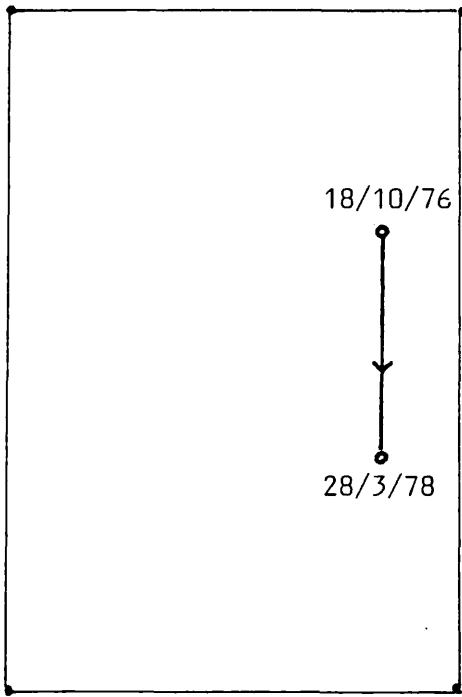
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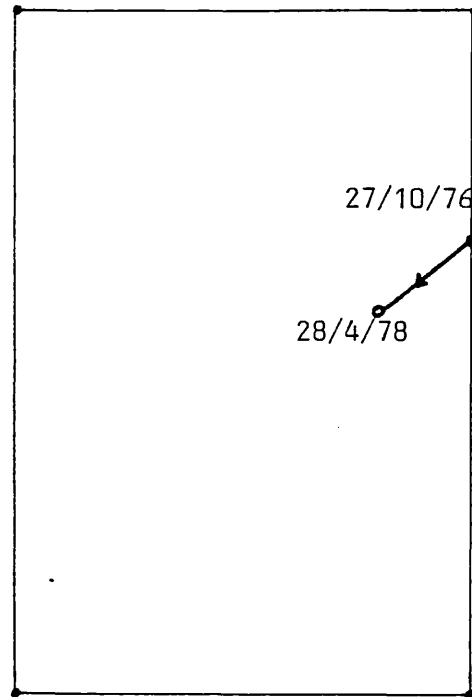
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Figure 7.2 (iii): Nebria brevicollis, (male), continued

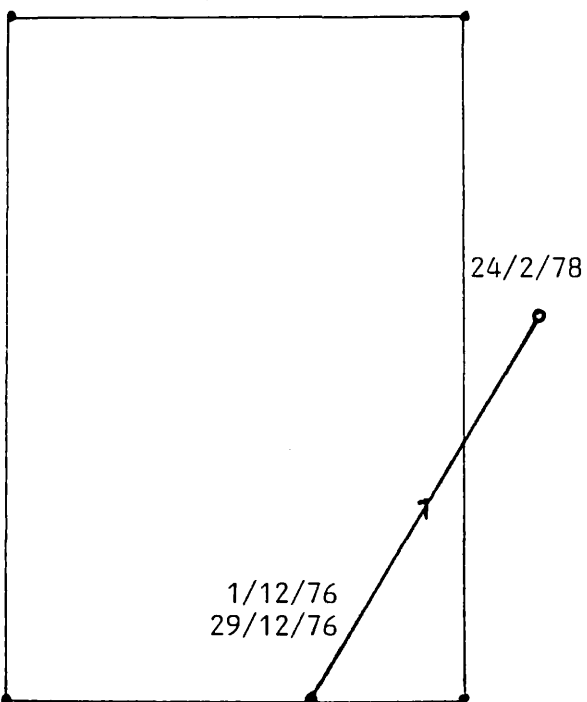
(x refers to a release point where different to capture point "0").



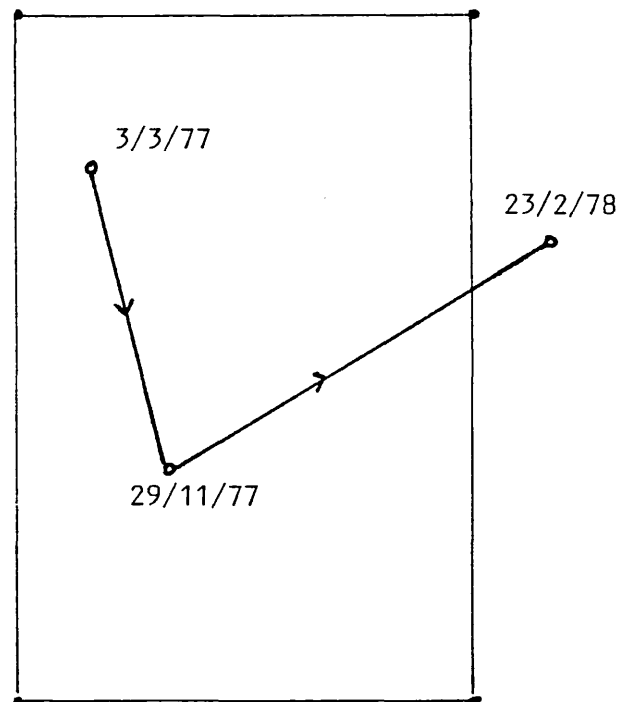
Ref. 1841



Ref. 1942



Ref. 1/239



Ref. 1/269

Figure 7.2 (iv) : Nebria brevicollis (male), continued

the grid boundaries. Of course, there is no way of knowing whether or not these animals have wandered extensively outside the grid, or that the "inside grid" restricted captures are an artifact. However, the possibility that some individuals at least have an activity range smaller than the grid cannot be ruled out.

7.230 Specimens from natural refuges

None of this species in this category.

7.240 Dissected females

Five marked females which were recaptured were unfortunately found to be dead on examination of the trap contents following heavy rainfall which flooded the traps. These were dissected and the condition of their reproductive system recorded:

- (i) Code 606: marked and released at trap point F6 on 14.4.1976; recaptured 27.9.1976 at F3. Nett displacement 45m, after 166 days. Corpora lutea dark, 2 eggs present.
- (ii) Code 921: marked and released at trap point E4 on 21.9.1976; recaptured twice, at F2 on both occasions, 25.9.1976 and 27.9.1976. Individual displacements 34m in 4 days, and nil in 2 days. Five eggs present,
- (iii) Code 801: marked and released at trap point C4 on 17.9.1976; recaptured at B4 on 27.9.1976. Nett displacement 15m in 10 days. Corpora lutea dark, 19 eggs present.
- (iv) Code 601: marked and release at trap point C6 on 14.4.1976; recaptured three times, at E7 on 25.9.1976, F6 on 6.10.1976, and E6 on 11.10.1976. Individual displacements 34m in 164 days, 21m in 11 days, and 15m in 5 days, respectively. Corpora lutea dark, 7 eggs present.

- (v) Code 747: marked and released at trap point G8 on 14.9.1976; recaptured twice, at E2 on 7.10.1976, and at E3 on 19.10.1976. Individual displacements 95m in 23 days, and 15m in 12 days. Eight eggs present.

These females were presumably ovipositing just prior to their last capture. The movements of specimens 601 and 747 are plotted in Figure 7.3.

7.300 Pterostichus madidus

7.310 Multiple Recaptures

This species produced few multiple recaptures, a product of the low recapture rate generally (see 5.340). Only nine male and three female beetles were captured on four or more occasions. These are listed in Appendix 7.3 and illustrated in Figure 7.4.

The displacements of the females are relatively short in length, as would be expected from Chapter 5.353. The males provide a strong contrast in the extent of their movements. It is significant that the three occasions when no displacement was registered the dates were well outside the breeding season (Nov and March). Low displacement in both males and females, with the exception of males during the breeding season, are in accordance with the general conclusions reached in 5.353.

Specimen 3/692 (a female) is of interest in that after 6 weeks activity in May and June, no nett displacement was achieved. The maximum displacement disclosed by the pitfall captures was only 20m. Actively localised behaviour (home range) has not been demonstrated

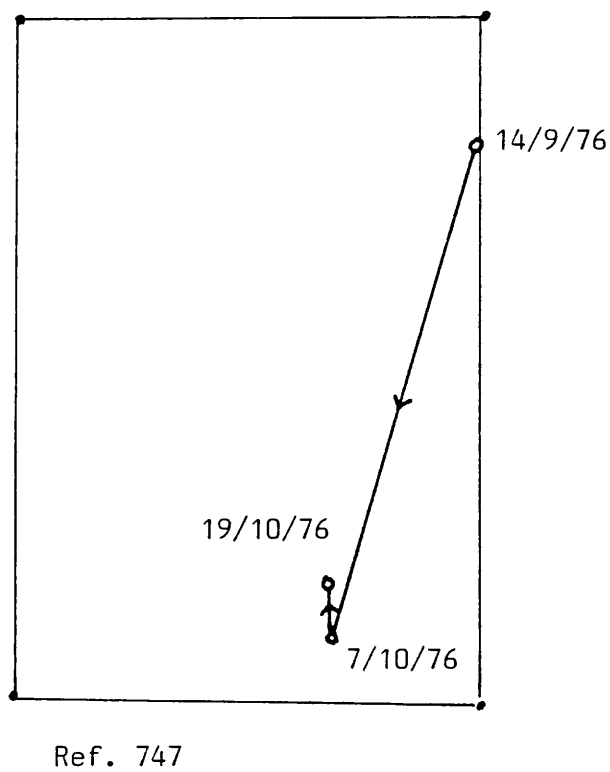
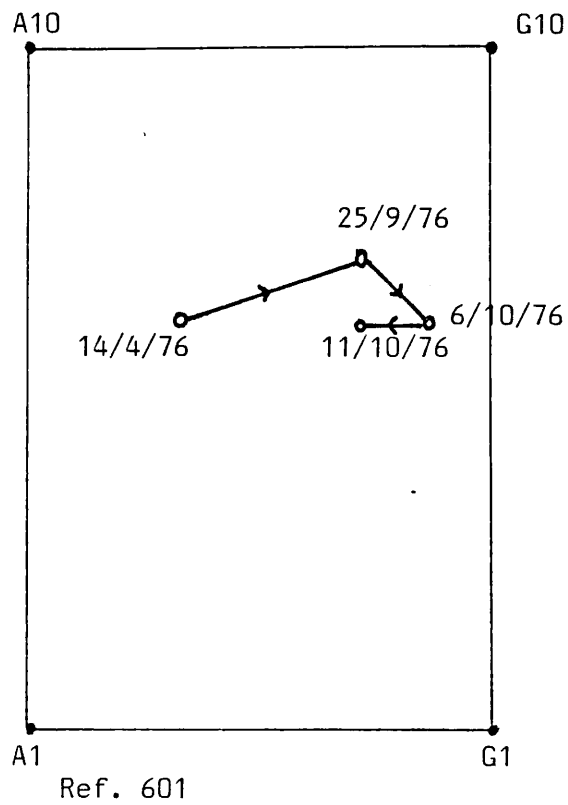
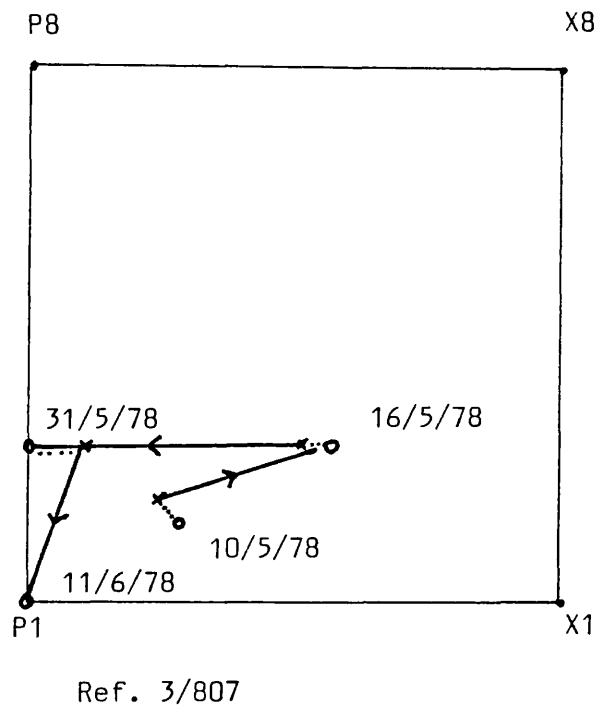
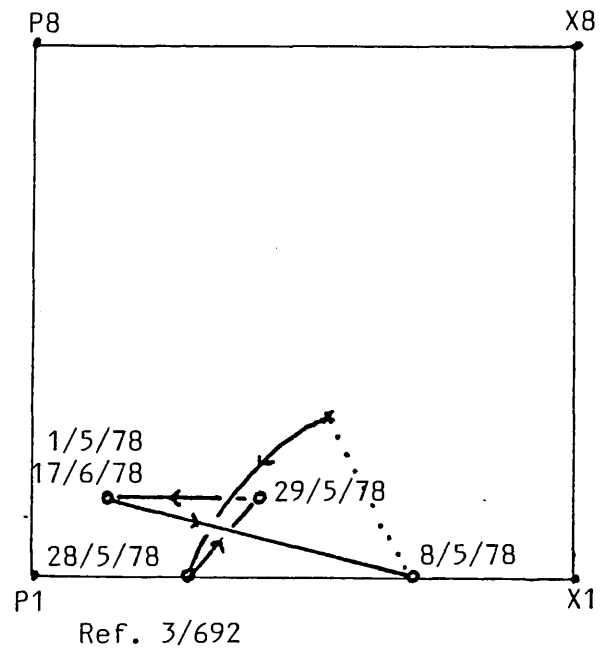
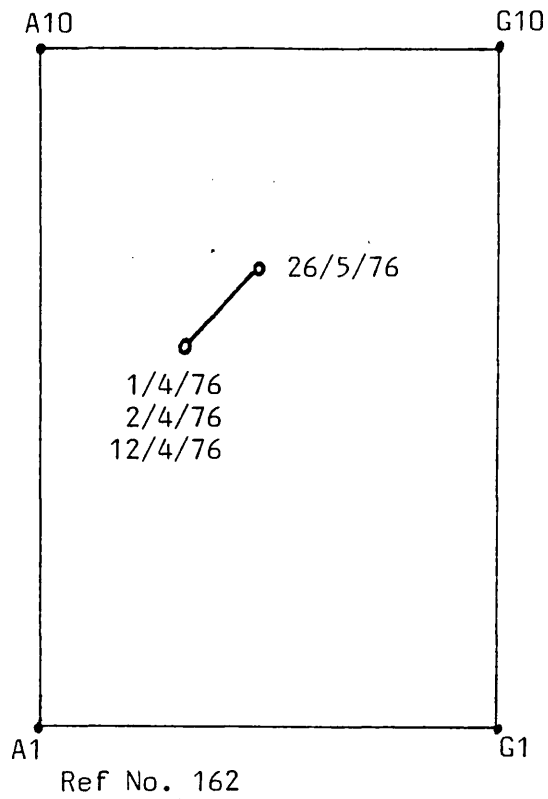


Figure 7.3 Nebria brevicollis : movements of ♀ beetles which were subsequently dissected.
(Scale 1cm represents 15m)



Scale:
1cm represents 15m.

Figure 7.4 (i) Pterostichus madidus : Movements of female beetles.
(X refers to release point where different to capture point "0").

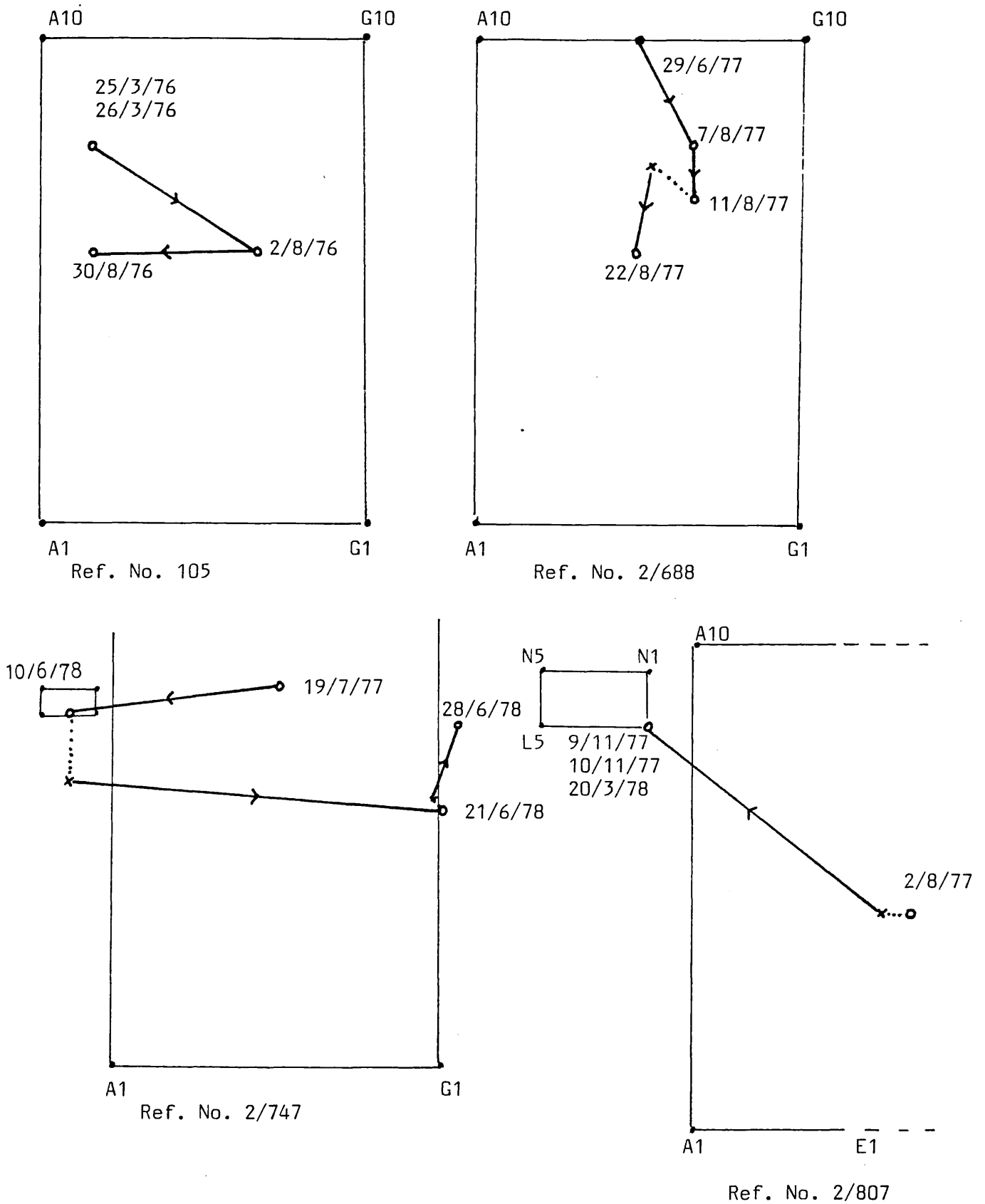
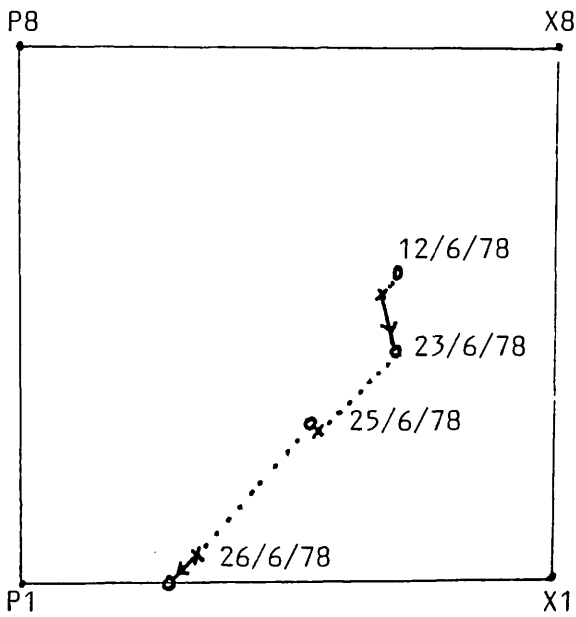
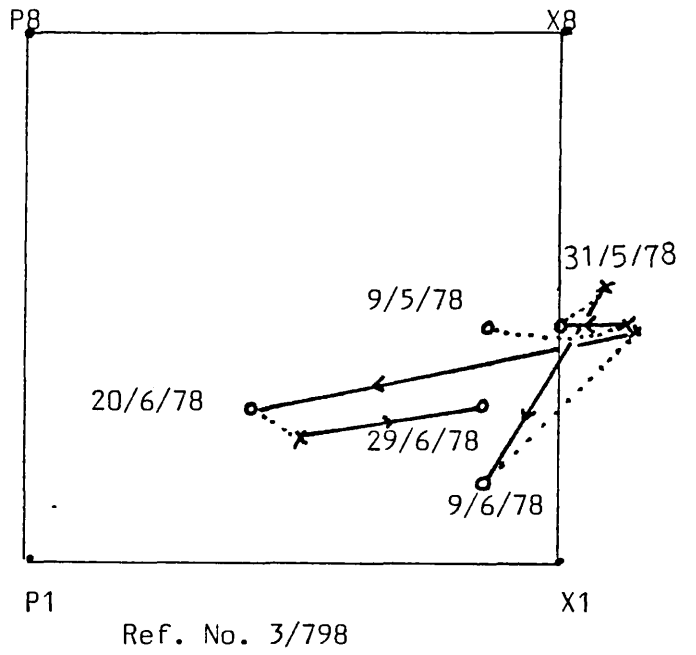
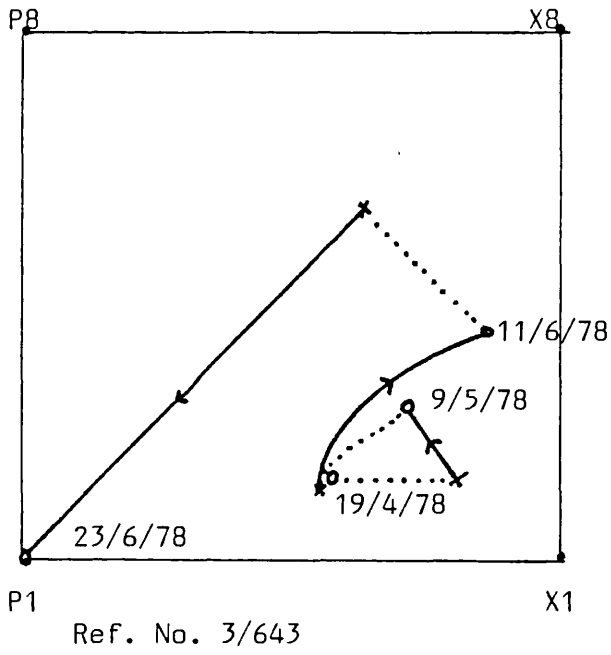


Figure 7.4 (ii) Pterostichus madidus : movements of male beetles

(X refers to release point where different from capture point "0").



Scale:
1cm. represents 5m.

Figure 7.4 (iii): Pterostichus madidus : male movements, continued.

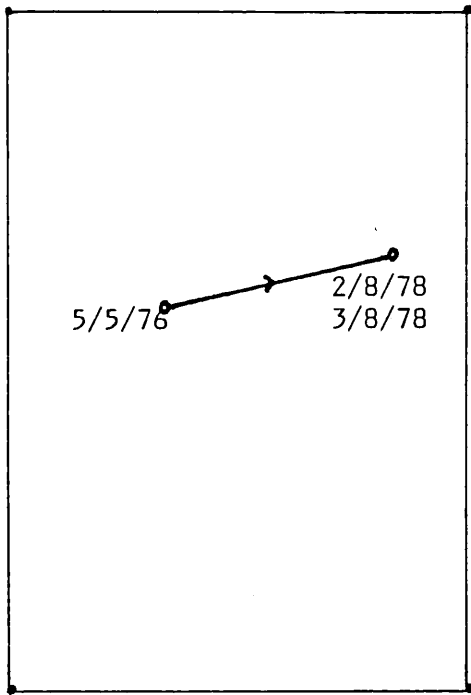
in this study (see Chapter 6) although such localisation suggests it. Similarly specimen 162 had displaced its location only about 22m after 8 weeks activity in April and May, and 3/807 produced a nett displacement of 11m after 4½ weeks activity, reaching a maximum displacement of 22m.

The movements of male beetles are more suggestive of the Nebria pattern (7.200), with large displacements occurring (although mostly in the breeding season) and frequent activity outside the main grid. Specimen 2/807 shows the low displacement rate in winter, and 3/643 the gradual building up of that rate as the season begins again, reaching a peak in June. In this species, unlike Nebria brevicollis, the older individuals appear to behave similarly to the new generation of adults.

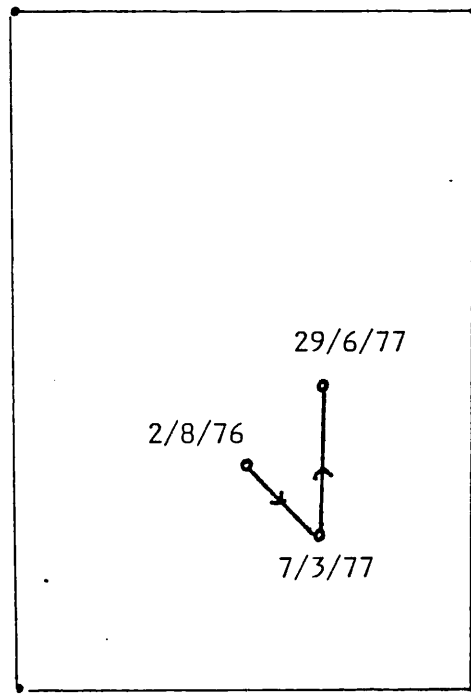
7.320 Long-lived beetles

In this category are 18 male and 24 female beetles which are known to have been active beyond two breeding seasons: 11 males and 17 females active in 1975 breeding season and again captured in 1977, and similarly 7 males and 7 females for 1976 and 1978. Only one of these animals (ref. 2/747) was considered in the preceding multiple recapture section (7.310), the rest were captured only infrequently.

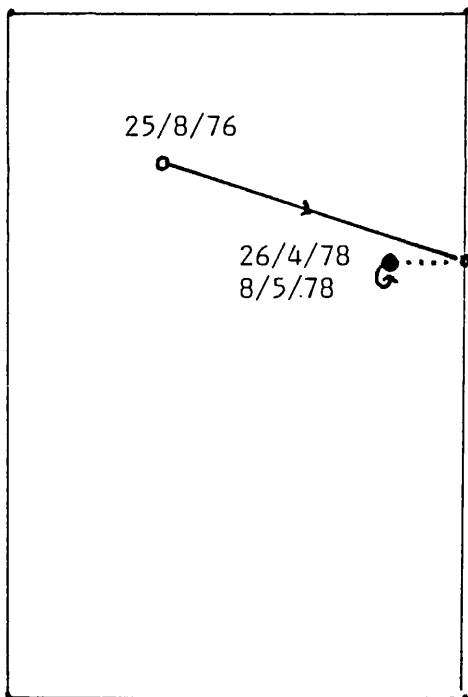
Of the first batch, the 1975 season beetles, three males and 6 females were last captured in 1978 - 2 of the males in June and August, thus are representative of the fourth breeding season animals referred to elsewhere (Chapter 4.300). The majority of recapture histories typically consist of two captures only - these have already been analysed in the earlier chapters of this study (Chapters 5 and 6).



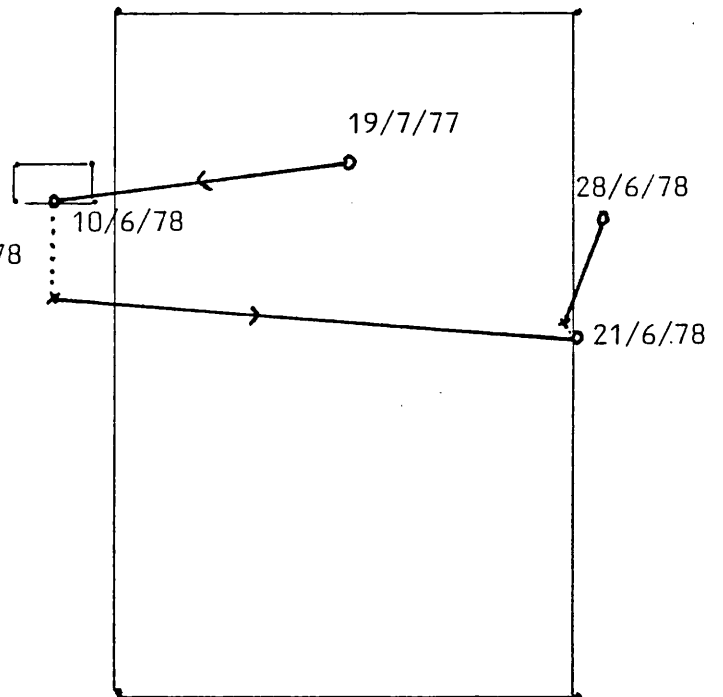
Ref. 327



Ref. 1/422

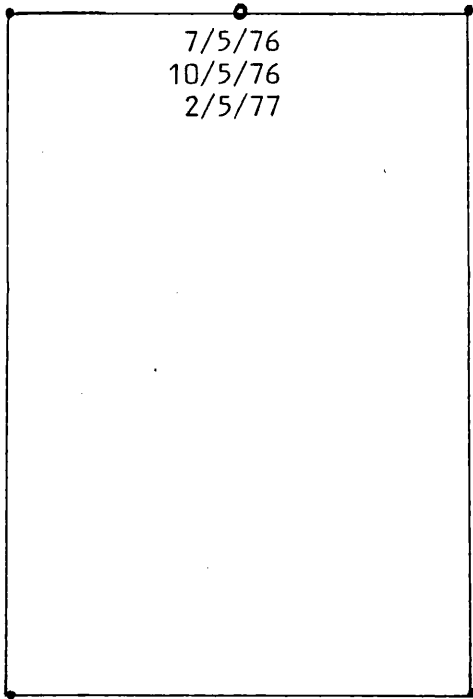


Ref. 100/738

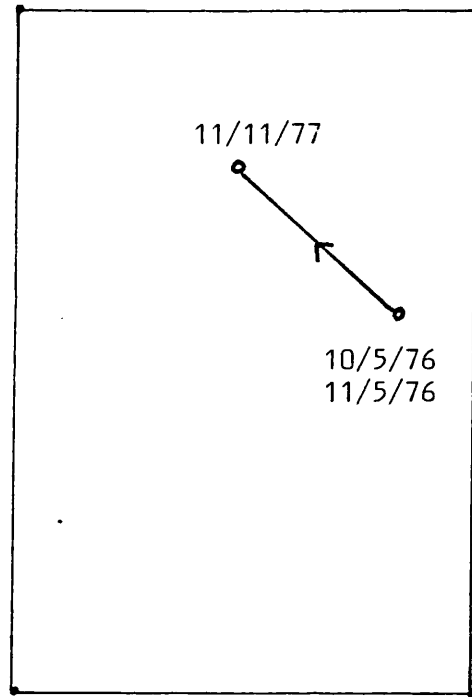


Ref. 2/747

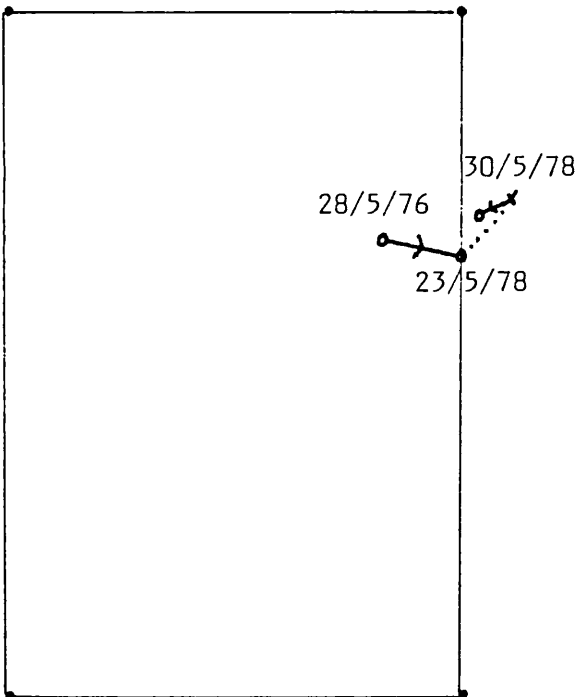
Figure 7.5 (i) : Pterostichus madidus (male) long-lived beetles : capture histories (X refers to release point where different to capture point "0"). (Scale: 1cm represents 15m).



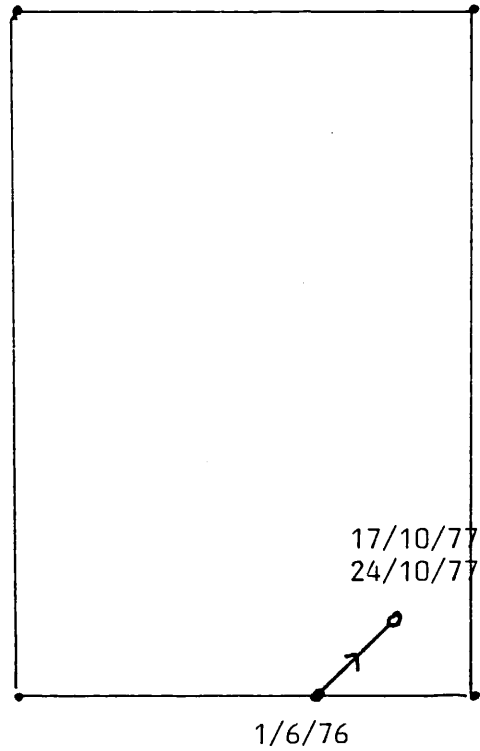
Ref. 433



Ref. 499



Ref. 697



Ref. 742

Figure 7.5 (ii) : P. madidus (female) (Scale: 1 cm represents 15m).

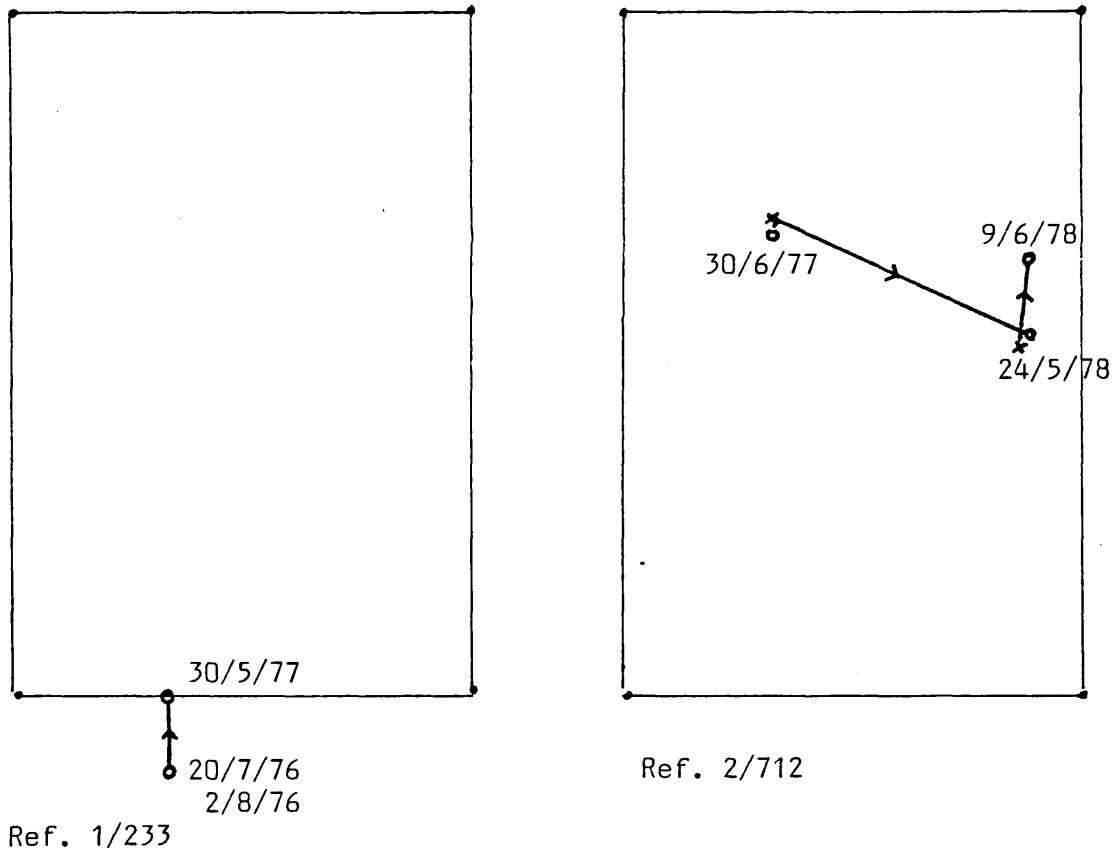


Figure 7.5 (iii): P. madidus (female) continued.

(Scale: 1cm represents 15m.).

Only the nine cases where three captures were made, and the one with four (as already illustrated in 7.310), are illustrated here (Fig. 7.5, details in Appendix 7.4).

These individual capture histories again illustrate the difference in activity between the sexes, particularly the female 433 which was only taken in one pitfall but over a time interval of nearly a year.

7.330 Specimens from natural refuges

Only two individual female P. madidus beetles were collected from a natural refuge, and neither were found again either in pitfall traps or beneath the log under which they were found. The log was located between locations E4 and E3 (see Fig. 2.2) near the centre of the grid. The disturbance of the environmental conditions beneath the log, or of the individuals themselves, may have contributed to the lack of re-use of the refuge.

7.400 Abax parallelepipedus

7.410 Multiple recaptures

Thirteen male and four female adult beetles were captured on four or more occasions (see Appendix 7.5 for details) and one illustrated here (Figure 7.6).

The main conclusion on the mobility of this species in Chapter 5.354 is that high displacement and high activity are associated with the first half of the capture season. This is certainly borne out by the movement diagrams. Activity again brings the animals into frequent contact with the grid boundaries, and it must be assumed that the normal range of activity of both sexes is greater than the

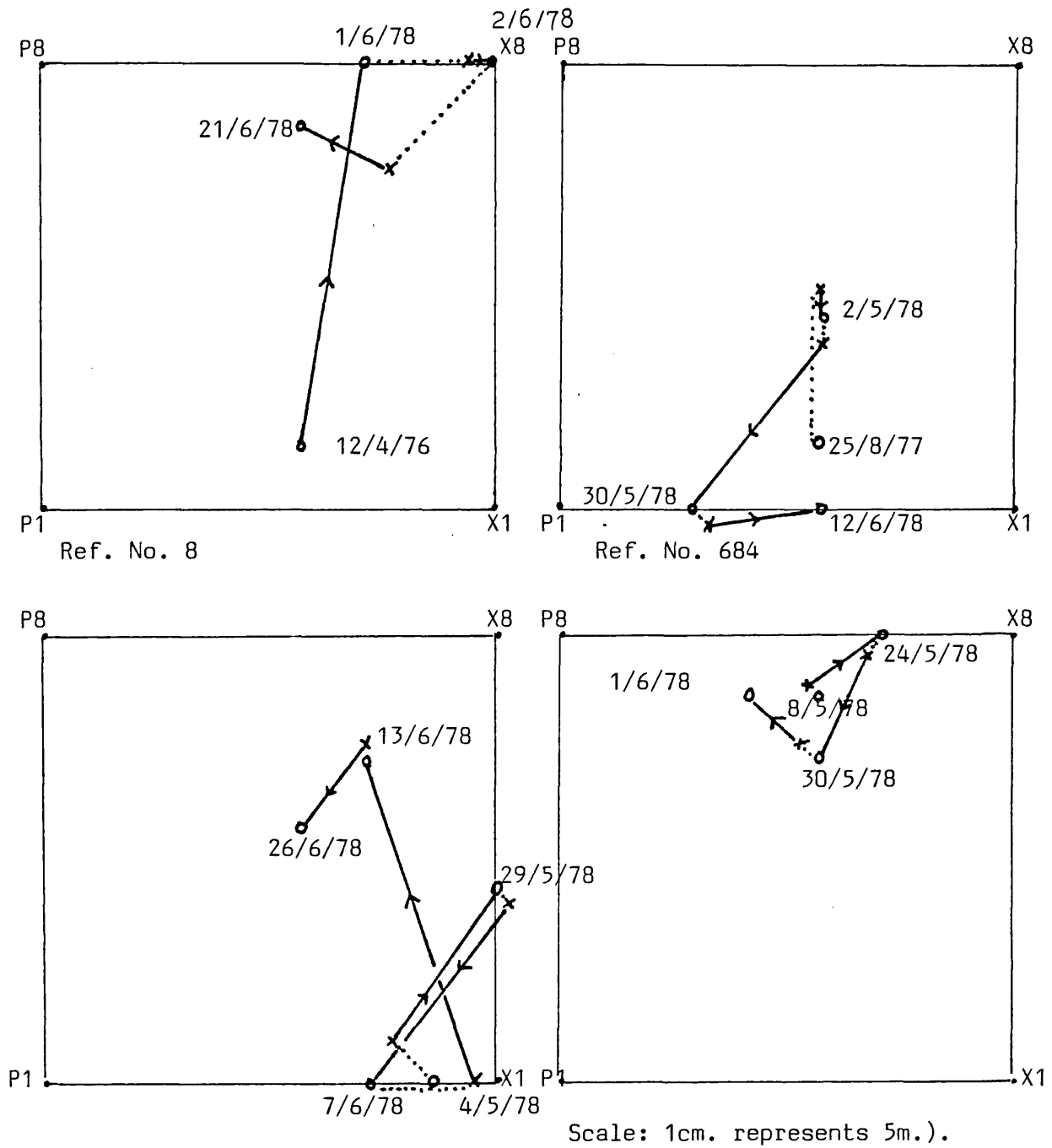


Figure 7.6 (i) : *Abax parallelepipedus* : female movements

(X refers to release point where different to capture point "O").

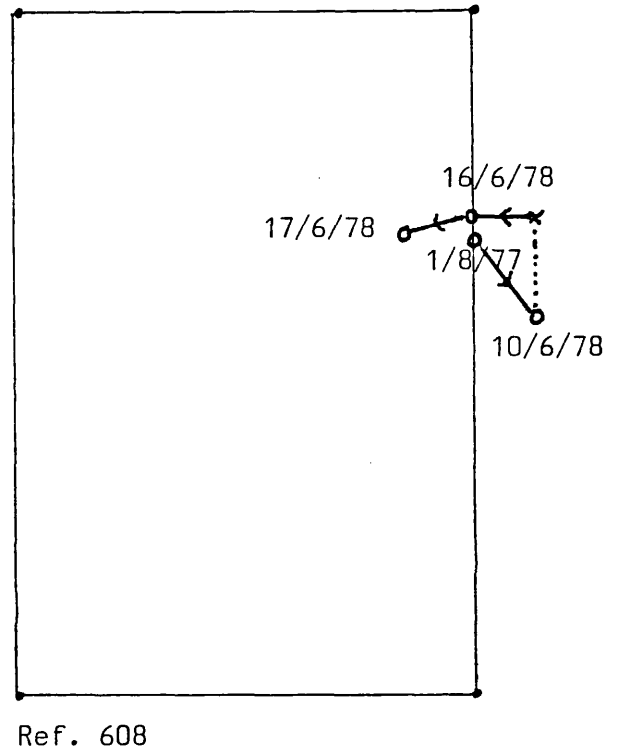
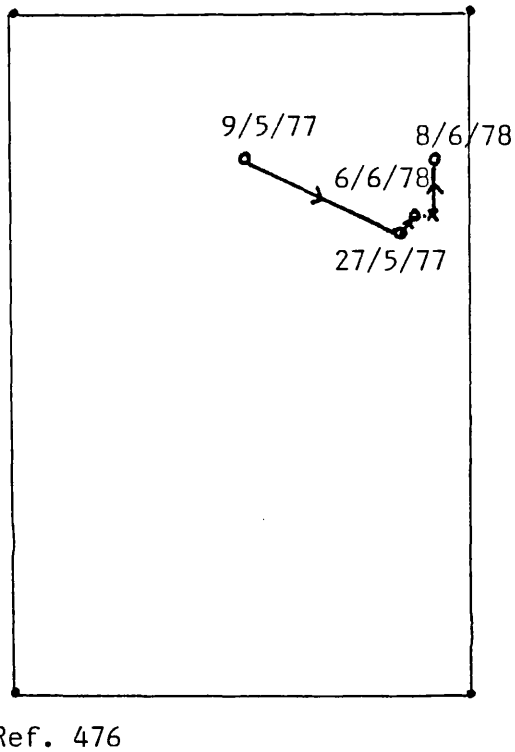
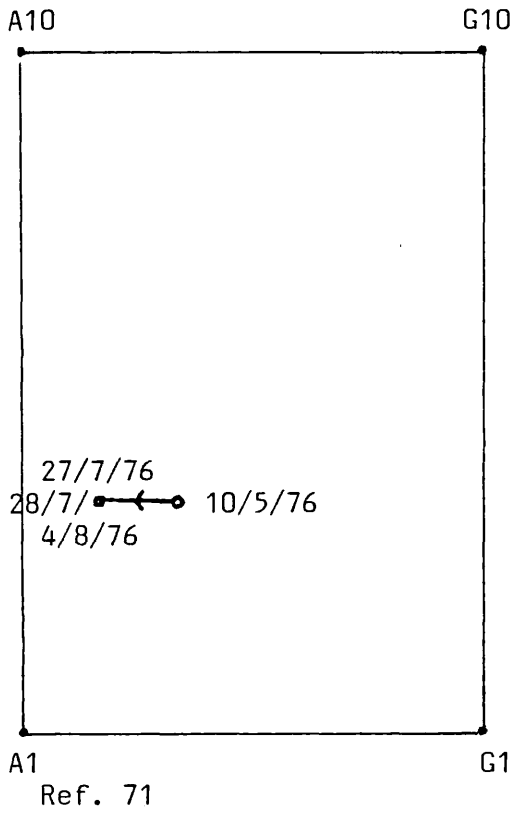
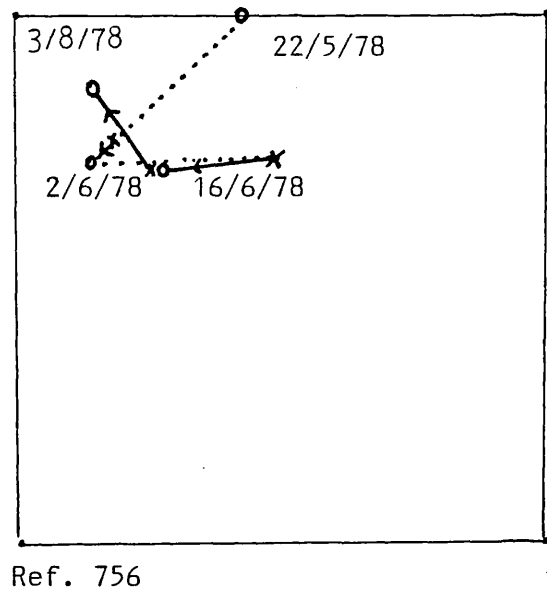
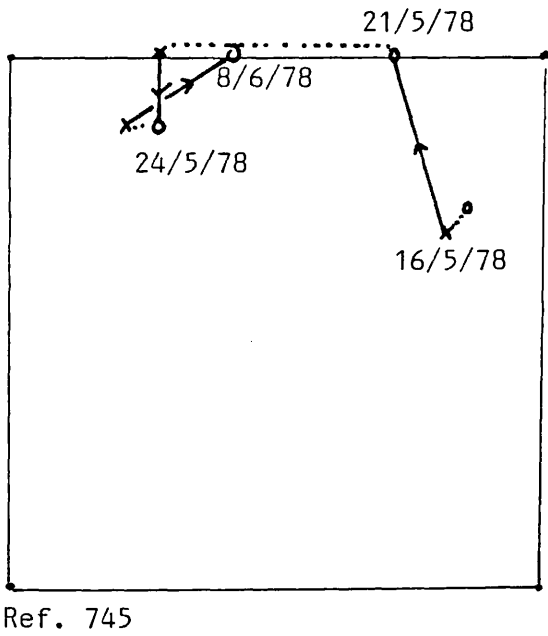
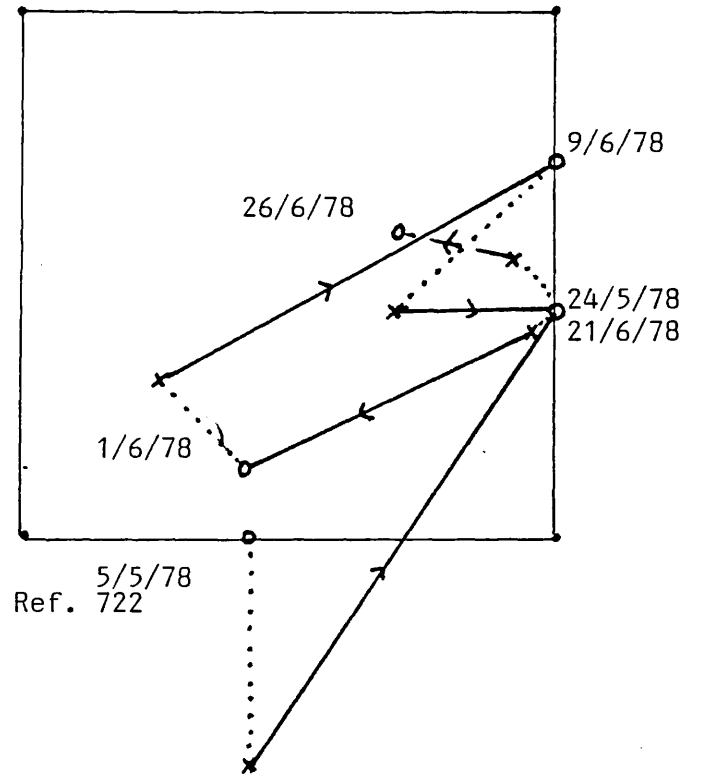
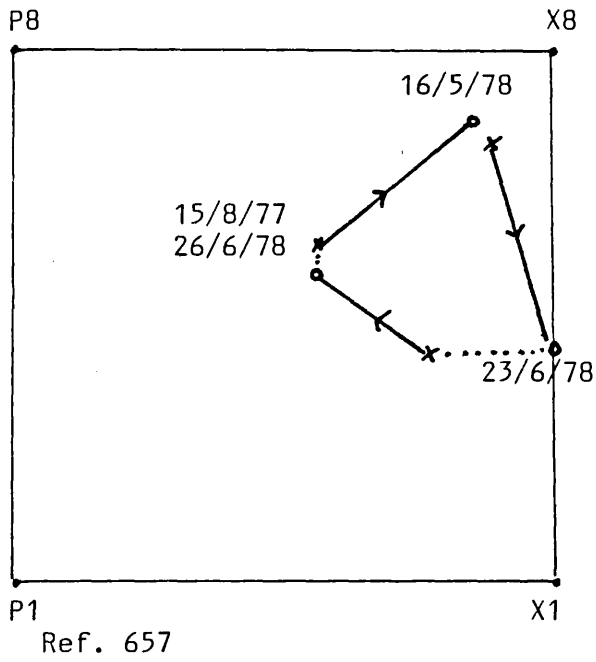


Figure 7.6 (ii) : Abax : male beetles (Scale: 1cm. represents 15m).



(Scale: 1cm. represents 5m)

Figure 7.6 (iii): Abax male beetles continued.

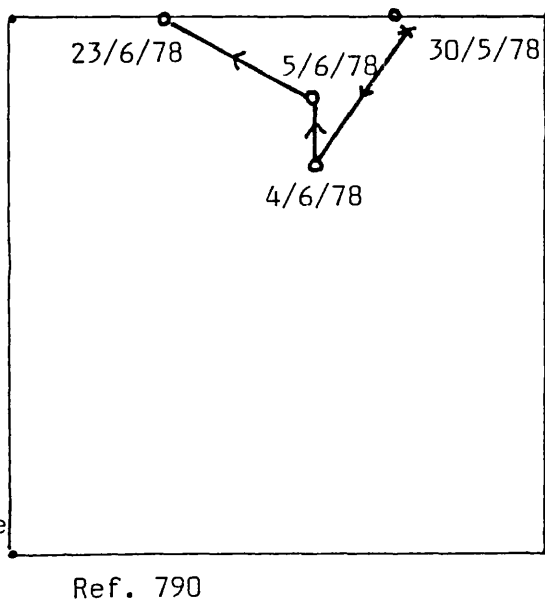
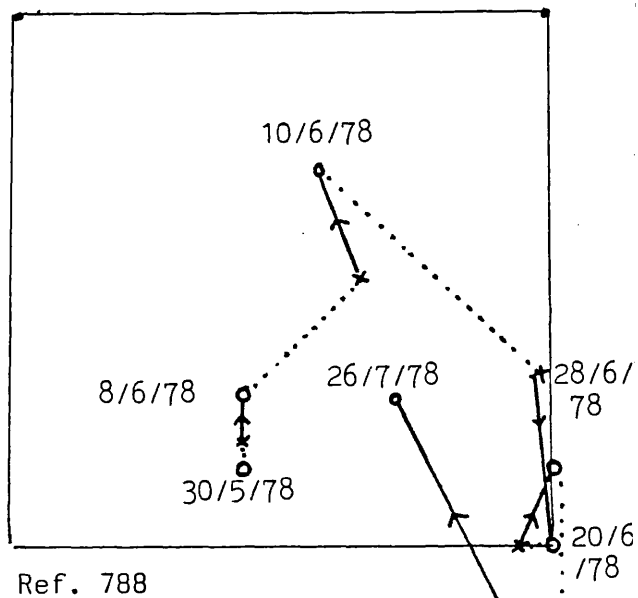
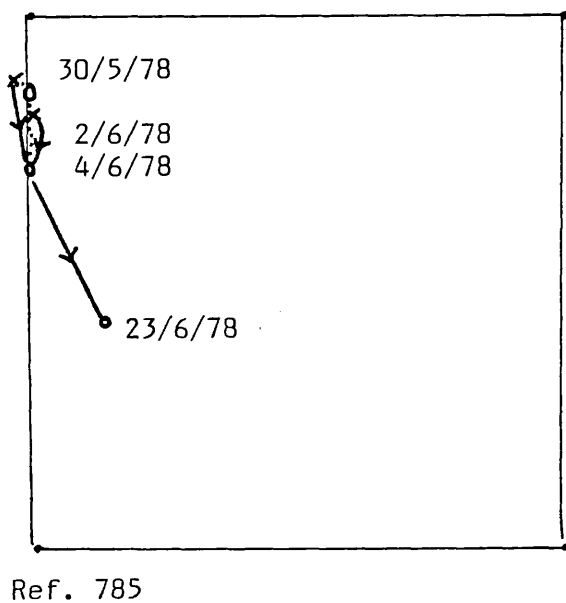
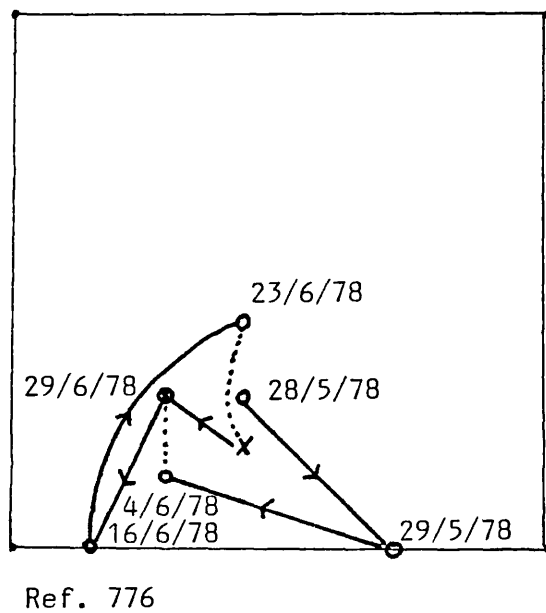
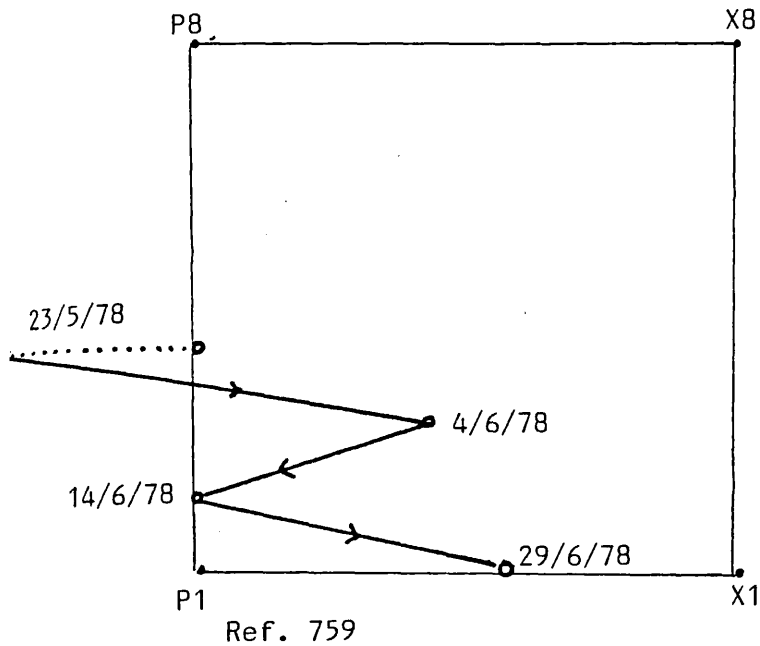


Figure 7.6 (iv): Abax male beetles. Continued

area of the grid.

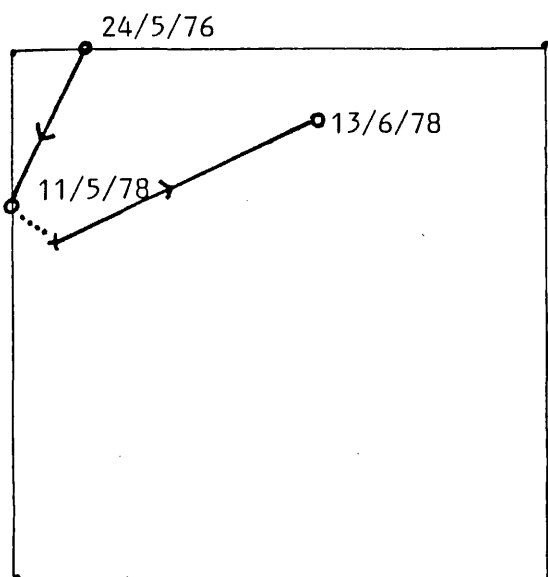
7.420 Long-lived beetles

As has already been discussed (4.400), the age categories of individuals of this species are difficult to deduce. Therefore, only beetles which were captured first in 1976 and later recaptured in 1978 are considered here. These certainly have lived into a second breeding season, and some may be entering a third. Seven males and five females fit here (see Appendix 7.6, and Figure 7.7). However, some were only captured twice, and are included as such in the preceding Chapters (5 and 6). These are considered no further.

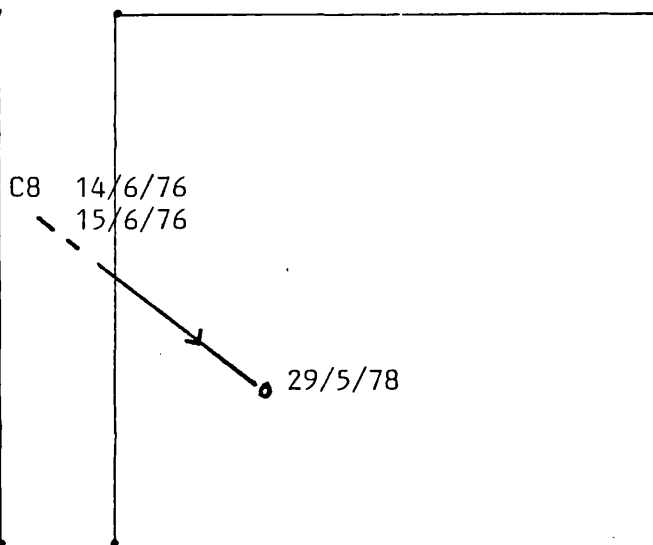
The diagrams of the movements of these beetles add no further information to that already discussed in 7.410, and the general comments applied throughout the chapter apply as regards the use of the grid area. Specimen 462, a female, is of interest as its first capture was as a callow adult. It was next captured more than 18 months later only 7 metres away from its release point, although two months later it was nearly 20 metres away. This greater displacement in May and June probably also occurred the previous year, but the nett resulting displacement after a full seasons activity was low.

7.430 Specimens from natural refuges

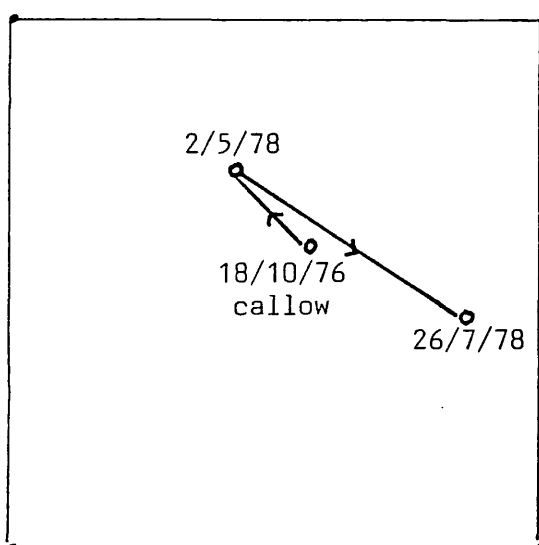
Three Abax beetles (2 males and a female) were taken from beneath rotting logs within the main grid area, and two of these (♂ and ♀) were released, marked, by the original logs. Only the male beetle was recaptured: log sited between D4 and E4 (see map in Ch. 2); beetle found and released 27.5.1977; recaptured in pitfall trap B9 on 11.8.1977. The beetle was pitfalled 81m from a natural



Ref. 131



Ref. 233



Ref. 462

Figure 7.7 (i) Abax p. long-lived females. (Scale: 1cm. represents 5m.).
 (X refers to release point where different from capture point "0").

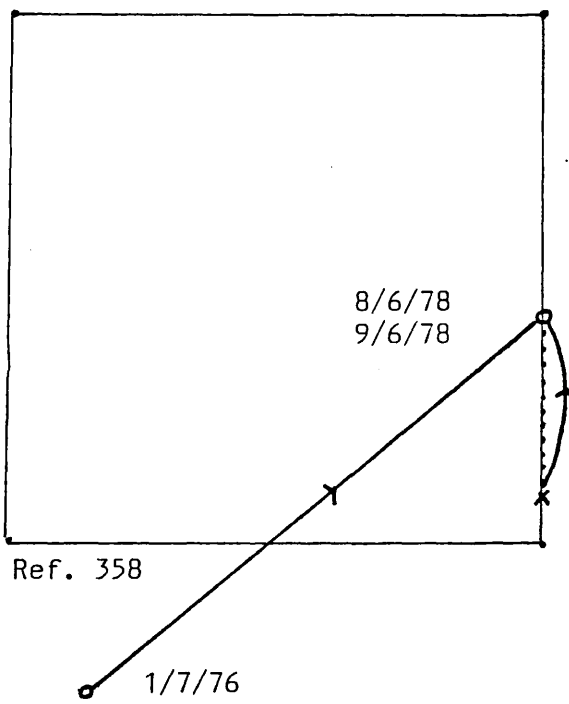
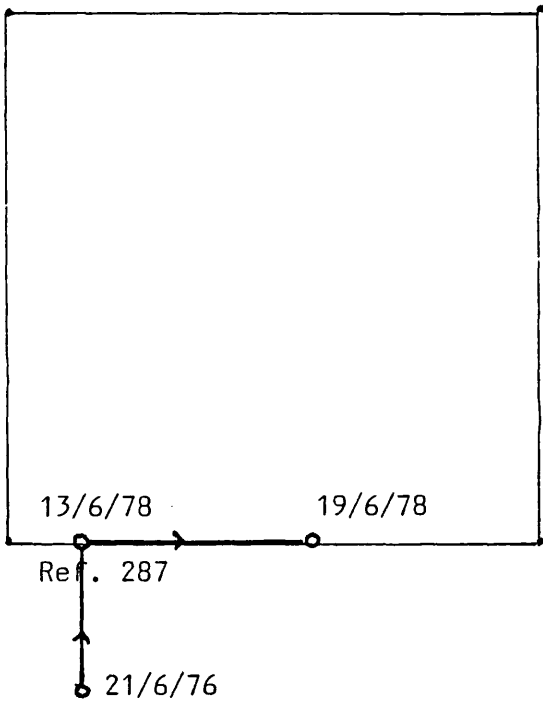
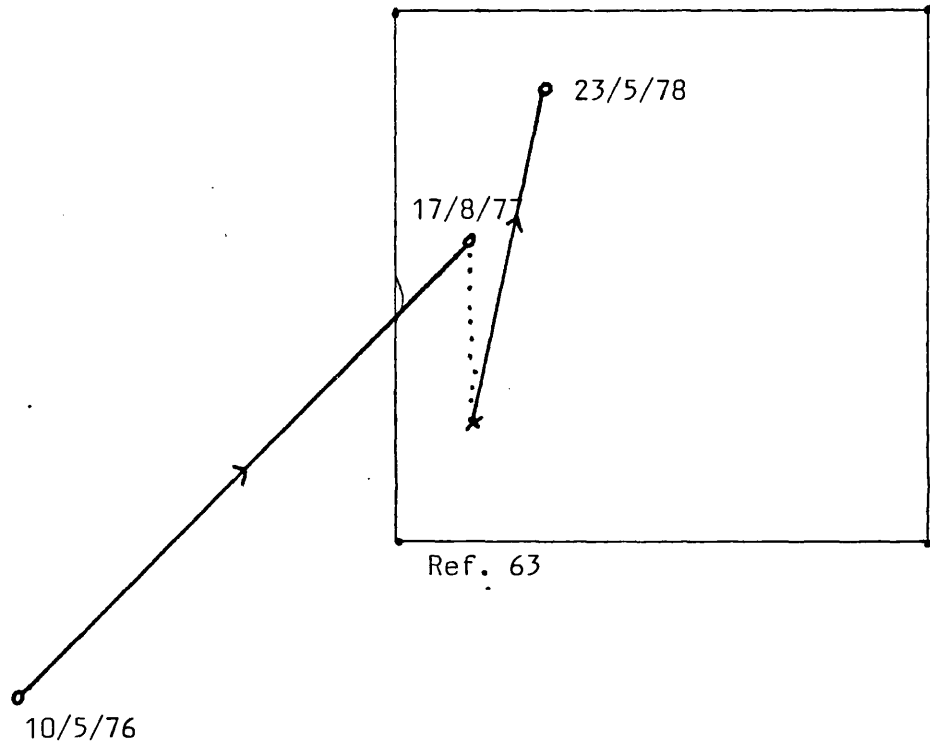


Figure 7.7 (ii) : Abax p. long-lived males

refuge in use 76 days previously - it was not pitfalled or found beneath logs subsequently. Again, the logs micro-environment would have been disrupted by searching for the beetles beneath. However, in this case, other beetles were found beneath the log subsequently.

On 1.7.1977, a female adult was found beneath an artificial refuge (a board placed some months earlier) between F6 and G7 trap locations. It was given an individual mark and released the same day next to the board - it was observed to push its way back underneath. This beetle was subsequently captured in a pitfall at S6 on 22.4.1978. Thus it was recaptured 15m away from its earlier refuge after 295 days. No further records of the individual were achieved, and the board was adopted by a colony of Myrmica ruginodis ants a few days following its original find there. The refuge was not therefore available to it for a long period.

7.500 Pterostichus niger

7.510 Multiple Recaptures

As no beetle of this species was recorded on four or more occasions, all illustrated individual capture histories in Figure 7.8 refer to beetles taken on three occasions. These fifteen beetles comprise 7 females and 8 males.

The general conclusion concerning this species (see 5.356) was that female displacement activity was greater than that of male. Although the diagrams appear fairly similar, the more restricted displacements are definitely all male beetles of 36, 148, 170 and 214. The large displacements seen in specimens of both sexes take the individuals concerned to the boundaries of the grid area, and

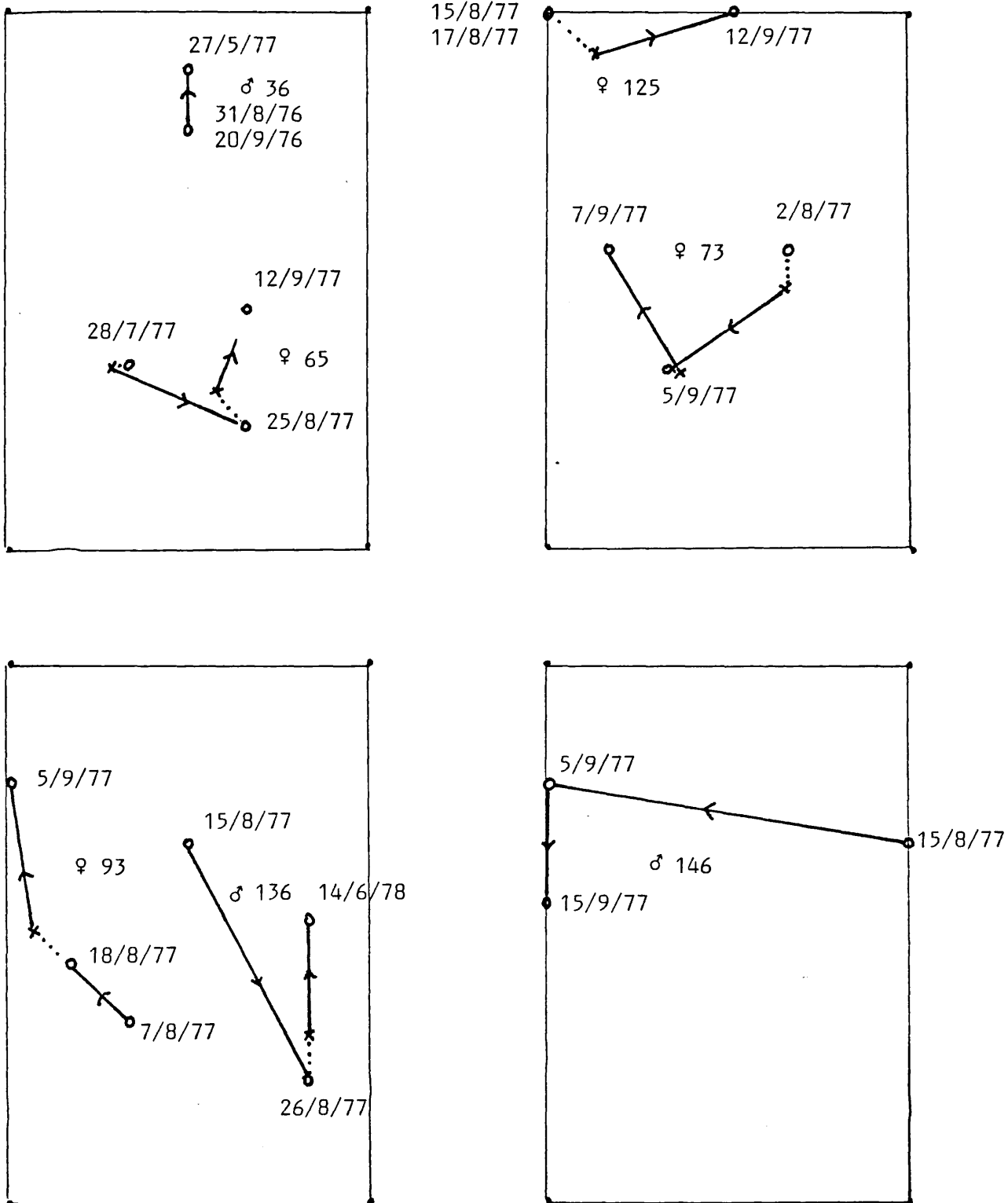


Figure 7.8(i) *Pterostichus niger* : Multiple recaptures

(Scale 1cm represents 15m.)

(X refers to release point where different to capture point "0").

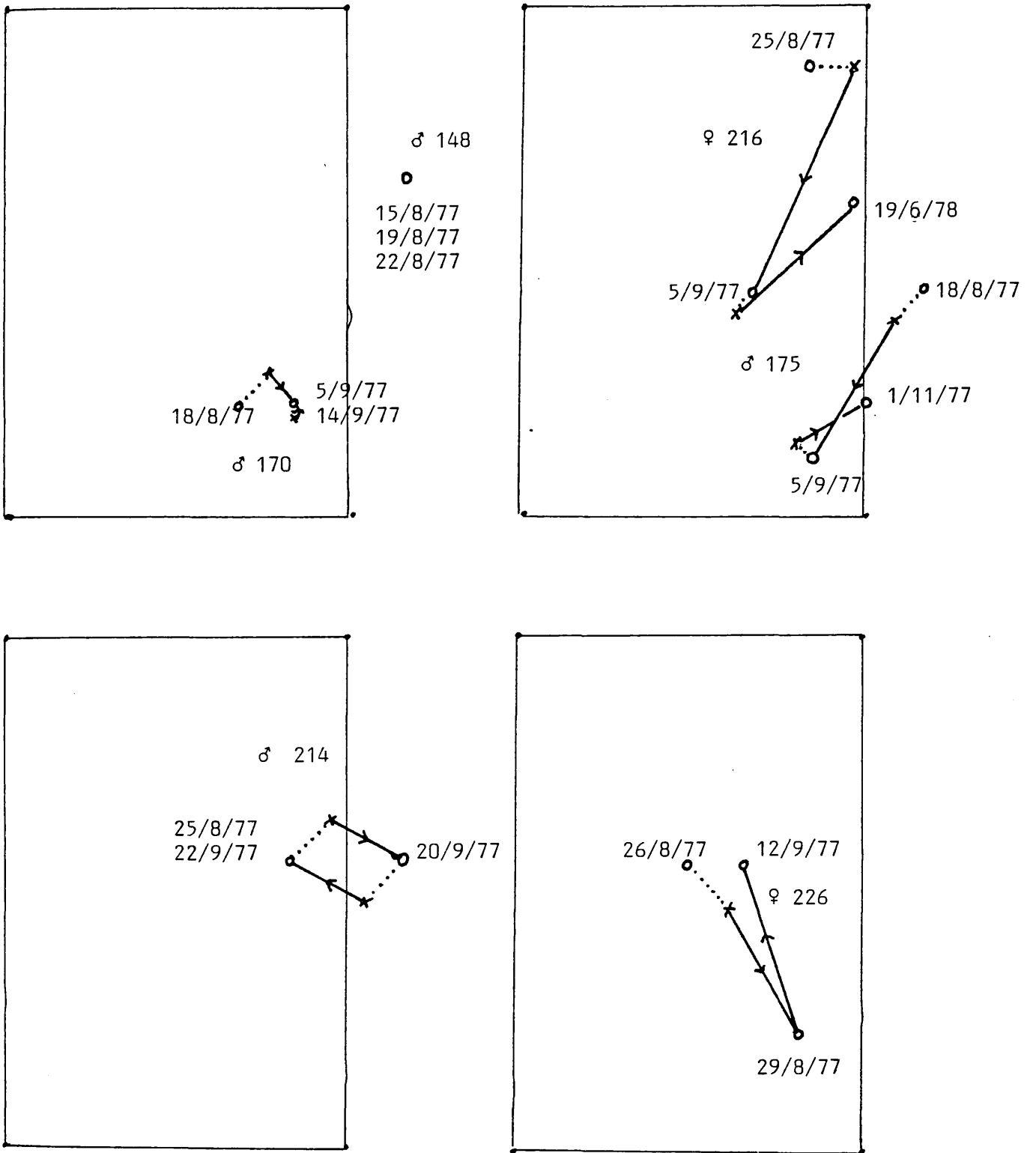


Figure 7.8(ii): *Pterostichus niger*, continued.

Scale: 1cm represents 15m.

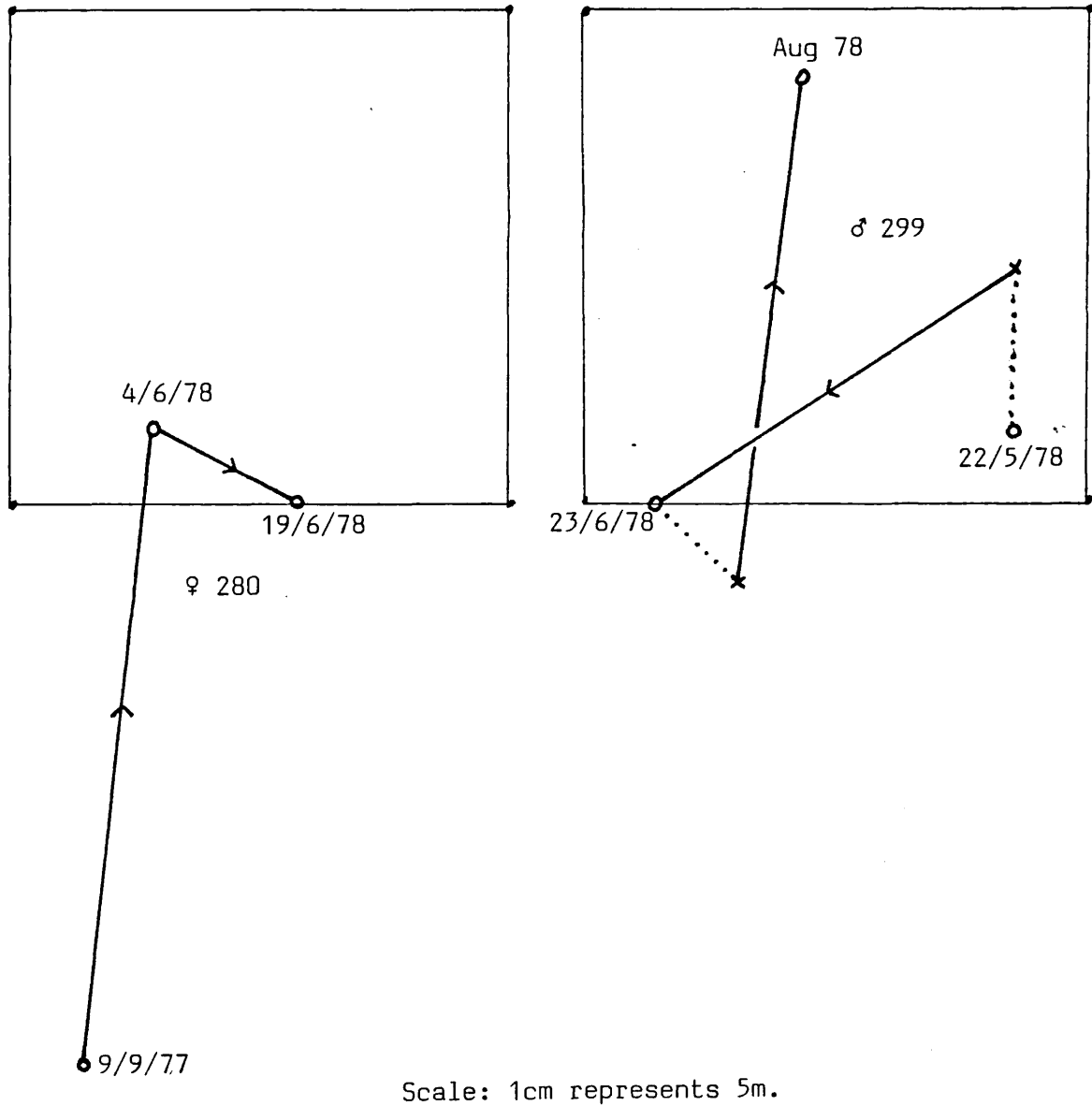


Figure 7.8 (iii): Pterostichus niger, continued.

thus their activity ranges are greater than the grid area.

7.520 Long-lived beetles

Only 10 beetles are known to have been active in at least two seasons : 6 males and 4 females, of which two males were 1976/77 and the rest 1977/78. Four of these, 2 males and 2 females, were recaptured on three occasions and are illustrated in Figure 7.8 with the multiple recaptures (36 and 136 ♂; ♀ 216 and 280). These long-lived individuals add nothing to the conclusions of the previous section.

7.530 Specimens from natural refuges

Three of this species, 2 males and one female, were taken from natural refuges on the study site - two from beneath logs on the ground, and the third (male) beneath the bark of an oak coppice stool 60cm above ground level. Each of these was marked and released near the point of origin, but only a log male was recaptured: released 25.5.1977 by the log between D4 and E4 pitfall trap locations; and recaptured in pitfall C4, 15m distant, 81 days later.

7.600 Carabus violaceus

7.610 Multiple Recaptures

Only two beetles were captured on more than three occasions and their capture records are illustrated in Figure 7.9. Both specimens are male (30 and 61). Little can be deduced from the progress of these beetles.

7.620 Long-lived beetles

Only six beetles, all female, were recaptured in a second year of trapping (see 4.600), five 1976-77, and one 1977-78, and only one

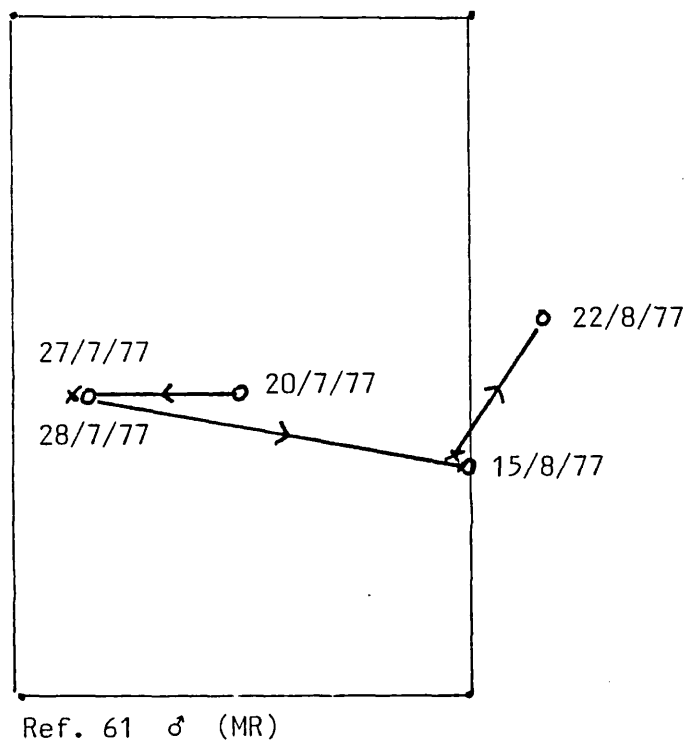
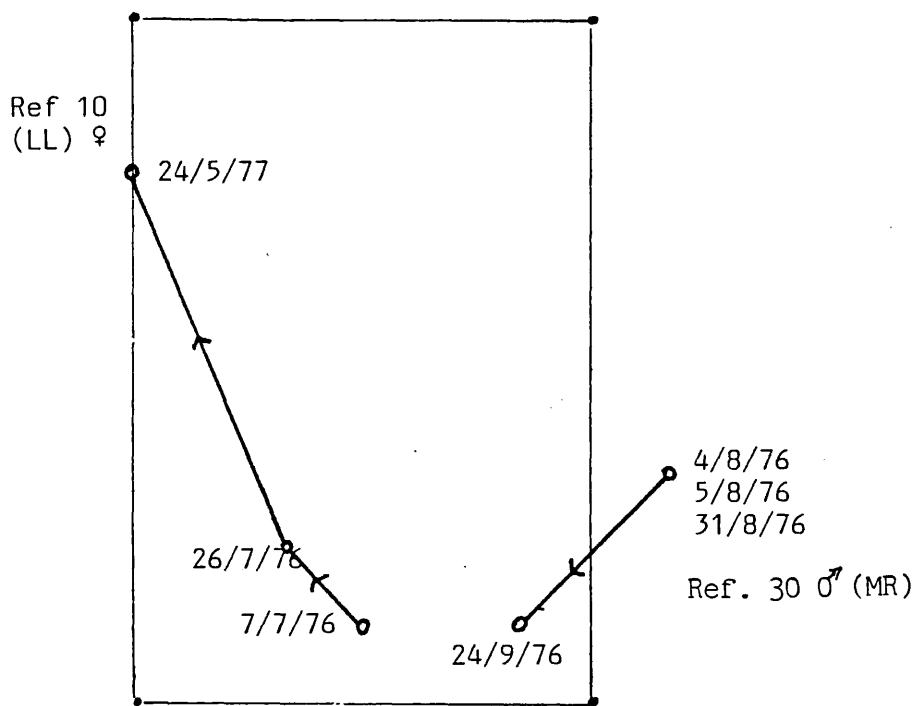


Figure 7.9 (i) Carabus violaceus: Multiple recaptures (MR) and long-lived (LL) beetles. (X refers to release point where different to capture point "O").

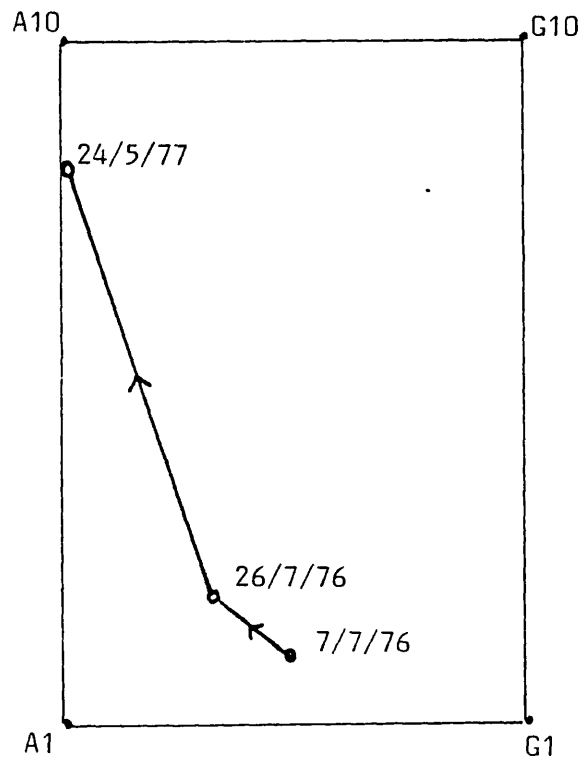


Figure 7.9 (ii) : Carabus violaceus: movements of long-lived female (ref. 10).

(Scale 1cm. represents 15m).

of the former group was captured on more than two occasions. The multiple recaptures both referred to single activity seasons. The single female recaptured on three occasions (specimen 10) is illustrated in Figure 7.9(ii).

7.630 Specimens from natural refuges.

None found.

7.700 Conclusions

In general, the capture histories of individual beetles confirm the general conclusions reached in the preceding chapters. Nowhere was direct conflict found. It would seem therefore that the conclusions reached by pooling individual capture results accurately reflect the behaviour of the individual beetles.

Chapter 8

General Discussion

8.100 Introduction

The main intention of this study was to examine the dispersive behaviour of certain common woodland ground beetles in relation to their life cycle, habitat, and population density. The interpretation of previous studies in this area of research has been much obscured by the variation in techniques used and lack of consideration of their full consequences. Available methods and the interpretation of their results have been investigated, partly using literature sources, and partly experimentally, and the results are presented in Chapter 3. Pitfall trapping combined with an individual marking technique was the approach selected. Pitfall trapping allows simultaneous sampling at a large number of locations, demonstrates activity, and is, as a result, superior to all other methods in the study of carabid mobility and dispersive behaviour. A coded mutilation marking technique based on that of Murdoch (1963) was used since the marks are permanent.

That pitfall catch size does not necessarily accurately reflect the number of beetles falling into the traps was clearly demonstrated in Nebria brevicollis where a potentially high percentage loss through escapes was demonstrated (3.430). This species was also shown to exhibit a significant drop in recapture rate following release if the beetles were left in the field traps^{or the laboratory} for a day or two following capture. The numbers of individuals in two other species, Pterostichus madidus and Abax parallelepipedus were rather small, and the results of the same analysis inconclusive. Two other possible features of pitfall catch interpretation were also investigated - attraction of beetles to the traps and the artificial concentration effect of the

traps, but the results were inconclusive.

The results of these experiments and the discussion of other aspects of pitfall trapping techniques clearly show the limitations of the method lacking the additional information provided by the use of individually marked beetles. Therefore, throughout this study, conclusions on activity and abundance are based on the results of mark-release-recapture experiments wherever possible.

Handling techniques and release procedure were also discussed and the general conclusion made that excessive disturbance of the beetles should be avoided by speeding up the marking technique and returning the beetles as soon as possible, and during their inactive period, close to the point of capture within the study site.

Clarification of the effects of pitfall trapping and mark-release-recapture on the beetles and their populations is a very important aspect of the study, and it is hoped that interpretation of the results has given full weight to this.

Having examined the methods, the next item to clarify before the dispersive behaviour of the beetles can be correctly studied and interpreted is the life histories of the five species selected for detailed investigation, and their position in the woodland system.

8.200 The Role of Carabidae in Woodland and Their Life Cycles.

8.210 The Environment of the Woodland Floor

The ground/air interface is not a sharp one in woodland. A shallow zone of vegetable detritus separates the free air from the soil below. This vegetable material consists of the partially rotted

leaves of the last year's leaf fall plus dry dead and dying twigs, branches and tree trunks that have fallen during the previous years. As these decay into the soil, a rich layer of humus is formed which covers, and mixes with, the underlying top soil. Rotting stumps of dead trees also add material. This then is the basic litter habitat.

Chauvin (1967) has brought together information about the microclimate of the woodland floor from a number of European authors, and the following description is based on his discussion. On the whole the floor of a wood receives only a low percentage of the sun's radiation, although green and infra red are much better represented than the other wave lengths. Following sunrise, the wood begins to gradually warm up - first the tree tops and, after about three hours, the layers nearest the ground. The diurnal range of temperature inside the wood is always less than in open country, particularly in the summer months and in deciduous broad-leaved woodland. Humidity is generally higher in woodland than outside due to the relatively low temperatures and stillness of the air, and increases during the day reaching its highest levels in the evening. This is the result of transpiration and respiration during the daytime. Wind and rain are greatly reduced by the canopy: about 50% of the rain falling on the canopy reaches the floor of a deciduous wood.

The nett effect is the production of a much stabler environment within the wood than outside - warmer in winter and cooler in summer. The litter shows these effects most of all the habitats in the wood. Of course, with deciduous woodlands there is a dramatic change in microclimate with the formation of the canopy in the spring and the

fall in autumn. However, the general picture still holds true even in winter - leafless trees still buffer the wind, and the litter layers are at their deepest.

In the early hours of darkness then, woodlands are more humid and warmer than open habitats, and it is significant that it is at this time that most of the woodland Carabidae show maximum activity (Vlijm et al, 1961; Greenslade, 1963; Breymeyer, 1966b; Williams, 1958; Thiele and Weber, 1968; Barndt, 1976).

8.220 The Carabidae

Thiele (1977) has recently brought together information on ground beetle life histories and incorporated it all into a classification of life history types which updates the earlier groupings of Larsson (1939) and Lindroth (1949). His five life history types are as follows:

- (i) spring breeders which have summer larvae and hibernate as adults,
- (ii) winter larvae, and adults reproduce in summer and autumn, but exhibit no adult dormancy,
- (iii) winter larvae, and adults emerge in spring and undergo aestivation (dormancy) prior to reproduction,
- (iv) flexible reproductive periods : spring and autumn reproduction can occur side by side in the same population; larvae develop equally well in summer and winter - reproduce at very different times of the year according to climate and weather,
- (v) development taking longer than one year.

It seems likely that as our knowledge of the family increases

then so will the classification into annual rhythm types. Thiele (loc.cit.) further grouped the types according to the regulation of the annual rhythms. More recent ideas on annual rhythms are given in Paarmann (1979).

Of the five species selected for consideration in this study, three (Pterostichus madidus, P. niger, and Carabus violaceus) are of the second type, and one each (Nebria brevicollis and Abax parallelepipedus, respectively) of the third and fourth types. The current study has produced results which agree over the first four species, but Abax is shown to have a more complex life history than group (iv) allows (see Figure 4.4).

The five species are nocturnal in habit and are to be found running inside, and over the surface of, the litter during the hours of darkness (Tipton, 1960; Williams, 1959b; Greenslade, 1965), and also to some extent upon the trunks and stalks of plants (Lloyd, 1963; Mason, 1972; Evans, 1975, and pers. com.; and personal observations). Daylight activity has been described in some of these species (Williams, 1958; Greenslade, 1961; Jackson, 1956; Nield, 1974), but these have largely concerned individuals in other habitats. During the present study only two daylight observations of activity were made - a female P. madidus at 10.10am on 14 April 1978, and a callow female N. brevicollis at 10.20am on 10 May 1978.

During the day the beetles are found beneath logs and stones on the ground, in the leaf litter and soil (see 3.240). Great Wood, however, possesses no stones large enough to serve as refuges, and few logs. Hand searching produced a few P. madidus, P. niger, A. parallelepipedus and Agonum assimile beneath logs, and only a

a single P. madidus in the litter. Thus the majority appear to spend the day in the soil. Soil sampling was not carried out because of the amount of work involved, but other workers have commonly found beetles in the soil (Frank, 1966; Mason, 1972).

Winter conditions result in the seeking of deeper refuges. The beetles generally burrow deeper into the soil than is usual in the active seasons, or else burrow into rotten logs and stumps of trees (Lloyd, 1963; Thiele, 1977; and personal observations). Rotting pine logs in Great Wood produced numerous Calathus melanocephalus and C. fuscipes - the former presumably having migrated from the adjacent field for the winter, and perhaps also the latter to some extent since that species is as common, if not commoner, in the field during the summer months. Agonum assimile, Abax parallelepipedus and Cychrus caraboides have all been found in small cells hollowed out in the soil beneath logs. In a visit to Argyll in 1977 Carabus granulatus Linn. and Pterostichus niger were both found in such cells beneath large stones in forests. P. niger was also found on one occasion beneath the bark on a dead oak coppice stool in Great Wood at a height of 60cm.

Apart from the species normally resident on the ground in the Wood, others are to be found solely on and beneath the bark of the trees and were never found on the ground, i.e. Dromius spp. Calathus melanocephalus has already been mentioned as a winter visitor, and Amara aenea have been found deep in the oakwood litter in mid-winter. In addition to the resident species and winter species, there are a number that are captured only in spring and autumn, and only as adults, never larvae. These are Amara spp, Agonum muelleri, A. marginatum and

Pterostichus angustatus (although the last two only as single specimens), which may be arriving or leaving as a result of overwintering, eg. Amara aenea, but may possibly also include dispersing individuals from other habitats. The nearest known localities for A. marginatum and P. angustatus are some miles from Great Wood and these species are unlikely to be merely overwintering.

The larger resident ground-living species all appear to be flightless. Abax parallelepipedus, Calathus fuscipes, C. piceus, Carabus violaceus, Cychrus caraboides, Laemostenus terricola and Pterostichus madidus were all found to possess vestigial or no wings at all, but the Leistus spp, Nebria brevicollis and P. niger all had fully developed wings. Flight has been recorded in N. brevicollis (Jackson 1956, Lindroth 1945) and P. niger (Lindroth, 1945), and presumed in Leistus spinibarbis (Lewis 1976), but these appear to be exceptional, and it seems more likely that the wings are usually non-functional. Flight must, however, be assumed to be regular for Leistus rufomarginatus considering its recent colonisation of southern England from the Continent (Hammond, 1974). On the whole though, flight may be discounted as a regular means of locomotion in most species, and particularly in the five currently under study.

So far larvae have only been mentioned as regards the types of life histories (see above). This is mainly due to the fact that much less is known about them. Generally those of the larger nocturnal woodland species are also nocturnal (Williams, 1959b; Nield, 1974; Luff, 1978). Larval Nebria are predominantly surface active and are frequently captured in pitfall traps (e.g. Tipton 1960; Penney, 1965; and Luff, 1975), although P. madidus and A. parallelepipedus larvae

are predominantly subterranean and are only taken sporadically (Williams, 1959b; Greenslade, 1965; Evans, 1969; Houston, 1970; Mason, 1972; Luff, 1973; Nield, 1974; and Kowalski, 1974). N. brevicollis being the only surface active larva, is thus the only one likely to play a significant role in dispersal.

Most ground beetles live a solitary hunting or scavenging life. Specialists do occur but the generalisation is sufficient here - the diets of the five studied species will be described later. Notiophilus and Elaphrus species are day-active in woodland and hunt their active prey (mostly springtails) by sight and have large ommatidia accordingly (Bauer et al, 1977). However, vision cannot be used in the nocturnal species, although they are capable of using it when day active in open habitats (e.g. Gradwell, 1954). In general, it appears that the beetles detect their food merely by chance contact. Mason (1972) found that four of the species under present study explored the soil surface with random movements, casting the antennae from side to side, and seized on any object that moved. Immobile food items are recognized by touch and taste (Mitchell, 1959; Manley, 1971; Evans, 1975; Thiele, 1977).

8.230 Nebria brevicollis

A species widespread in the Western Palaearctic, being found as far north as southern Norway and Sweden, south to the Mediterranean coasts, and east to Moscow and Caucasia (Turin, et al, 1977). The beetles are very common in woods, but less so outside them, preferring the open litter areas beneath deciduous trees (Lindroth, 1945; Williams, 1959b; Greenslade, 1964c; Evans, 1975). Both adults and larvae are surface runners (Williams, 1959b; Penney, 1966) and the adults were

the fastest runners for their size range tested by Thiele (1977). The predominant food of both adults and larvae is small insects, spiders, and mites, but they will also take woodlice (Davies, 1953; Evans, 1964; Penney, 1966; Sunderland, 1975). Seasonal fluctuations in composition of prey are small (Penney, 1966). The relative scarcity of the litter and soil fauna during the midsummer months (Manns, 1967; Mason, 1972) is one of the reasons put forward for the aestivation period (Penney, 1966).

The life cycle follows Thiele's (1977) type 3, the adult beetles emerging from the pupa in the spring and entering aestivation prior to reproduction in the autumn. Larvae were pitfalled from October until early May, the three instars peaking in January, January-March, and February-March respectively. Adults recently emerged from the pupae are active in May and June before entering aestivation. Activity resumes at the end of August and early September, by when the reproductive organs are fully developed and mating and ovipositing occur well into the winter months. A significant proportion of adults survive the winter and resume activity in the spring, but the reproductive organs of the females at least do not become active again until the autumn. The beetles re-enter aestivation before the new generation has emerged, but resume activity once again at the same time as the new generation. The proportion of adults reaching a second breeding season was at least 22.0% for 1975-76 and 5.4% for 1976-77. Three individuals were recorded entering a third breeding season. Dissection studies combined with individual marking have demonstrated that eggs may be produced by an individual in two consecutive years (see 4.200 and 4.820).

8.240 Pterostichus madidus

This species is restricted to central western Europe, being found in Britain, France, Belgium, the Netherlands, Germany, Austria and extending to varying extents into the neighbouring countries (Thiele, 1977; Turin et al, 1977). It is a eurytopic species, and has been recorded in forests, cultivated fields, grasslands and moorlands (Greenslade, 1964c, 1968; Neumann, 1971; Evans, 1975). The larvae are mostly subterranean (Williams, 1959b; Greenslade, 1964c; Houston, 1970; Luff, 1973) and the adults appear to be so also to some extent - they have been described as living in burrows both in laboratory soil-filled containers (Frank, 1966; Mason, 1972; and this study) and in the field (Mason, 1972; Kowalski, 1974). Evans' (1977) studies have shown P. madidus to be a powerful "wedge pusher", and the legs are adapted more for pushing than running. Thus the beetles are better adapted to moving within the litter than over it.

P. madidus is a general predator and scavenger, taking both living and dead animal and plant material. Studies of the gut contents have found a very wide range of invertebrate food material, as well as plant material such as grass leaves and moss fragments (Davies, 1953; Mason, 1972; Luff, 1974). Mason (loc.cit.) found that plant material was taken especially in midsummer. Luff (loc.cit.) also examined the gut contents of the larvae and found that they took similar food to the adults, although no plant material was found.

The life history follows Thiele's (1977) type 2 with adults reproducing in the summer and autumn, but exhibiting no dormancy, and producing larvae which overwinter. Larvae were found in small numbers in the pitfall traps from the end of September until May, and even

June in one case, with the three instars peaking in October–November, November–March, and March–April respectively. Adults recently emerged from pupae are most abundant in July and August. Some of these begin breeding in that year, although some at least breed first in the following year. Overwintered beetles become active again some months before the new generation appear, and apparently resume breeding soon after their emergence from winter inactivity. Individual marking studies showed that fewer individuals successfully reach their second breeding season as compared with N. brevicollis (at least 2.97% in 1975/76 and 4.4% in 1976/77), but that also a good proportion of these achieve a third breeding season (30.2% - 13 individuals of the 1975/76 group reached 1977, and 16.1% - 9 individuals of the 1976/77 group reached 1978), and seven of the 1975/76 group were even present in a fourth season (0.5% of the total marked prior to the 1976 pupal emergence). Working in the relatively colder north of England, Luff (1973) found only a single beetle out of 6284 marked that had survived more than one winter in the adult stage. Breeding in more than one season was clearly demonstrated by dissection and marking studies. A slight increase in catch size each autumn may be extra feeding activity prior to winter inactivity (see 4.300 and 4.820).

8.250 Abax parallelepipedus

The distribution of Abax parallelepipedus is distinctly central European. It is found as far north as Scotland and the southern tip of Sweden, south to northern Spain and Italy, east to Moscow, and west to Ireland (Turin et al, 1977). It is most commonly found in woodland and forest situations where the leaf litter has a very loose structure. The highest frequencies are found in areas where an open

canopy has produced a field layer of bracken and scrub such as at the edge of Woods, clearings or in hedgerows (Drift, 1951; Greenslade, 1964c; Haines, 1973; Thiele, 1977).

Like P. madidus, the larvae are mostly subterranean (Evans, 1969; Mason, 1972) and, again like P. madidus, the adults spend much time within the litter and soil layers. Evans (1977) found it to be a powerful pusher and burrower and it has been found beneath the soil surface in the laboratory in large and regularly used burrows (Frank, 1966; Mason, 1972). Its burrowing habit is also seen in studies by Kowalski (1974) where beetles found and attacked winter moth pupae buried 2-4 inches (5-10cm) in the ground. The similarities with P. madidus do not stop here. Abax is a general predator and scavenger, but takes more of larger prey such as caterpillars and molluscs (Drift, 1951; Davies, 1953; Dempster, 1967; Mason, 1972). Drift (loc.cit.) also found traces of mammal or bird blood in one gut examined, presumably derived from feeding on a dead animal. Mason (loc.cit) could find no seasonal variation in the gut contents. Thiele (1977) says the larvae live exclusively on earthworms.

The life cycle has been described by a number of authors but none have investigated it in detail. Consequently it is but poorly understood. Thiele (1977) placed it in his fourth grouping (8.220) where the reproductive period is flexible. Both spring and autumn reproduction occur in a single year, and the larvae can develop both in summer and winter conditions. However, adults and larvae are much less tolerant of winter conditions than the preceding two species, as is seen by the small numbers pitfalled between November and March. Kowalski (1974) found adults down to 20cm, and larvae usually at

greater depths, in cells in the soil during the late autumn and winter.

A proposed life cycle is illustrated in Figure 4.4. Overwintered adults begin ovipositing in May and some at least continue doing so into August and possibly September. The earlier eggs have reached the third larval instar by the onset of winter, and pupate the next spring producing immature adults in May and June. Later eggs overwinter as such or as young larvae and do not reach the third larval stage until the following June, resulting in a second peak in immature adults in August-September. Both groups of immature adults may overwinter, but the earlier batch may have reached maturity and started to breed before the onset of winter. Thus there are two larval cycles, but they are not separate, they each result in individuals which in turn produce larvae in both cycles. However, the later eggs take two years to produce mature adults, whereas the earlier ones take one. Although two distinct cycles have been described by a number of authors (e.g. Drift, 1951; Loser, 1970; Mason, 1972; Haines, 1973), none have pieced the information together to produce a picture of how the system works. The above description appears to work for the other authors' data.

In colder latitudes, the shorter summers further restrict the activity period of the species and so few, if any, of the early callows reach maturity in time to breed in their first year. The two year cycle predominates (see Houston, 1970, for example).

8.260 Carabus violaceus

This species has a Palaearctic distribution (Lindroth, 1945) and

is commonly found in both woodland and grassland habitats (Greenslade, 1964c; Pollard, 1968; Evans, 1975). Both larvae and adults are surface active (Evans, 1969). The adults are structurally adapted to fast running (Evans, 1977), and their heavy powerful bodies enable them to hunt in restrictive habitats (Forsythe, 1983).

Adults have been observed feeding on young harvestmen (Sankey, 1949) and rotting apples (Hart, 1884). Davies (1953) examined the gut contents of a number of adults but all except one contained only liquid. The exception contained a piece of arthropod trachea. Thus it would appear that this species practices pre-oral digestion and only takes in liquid food. The diet has been further elucidated by serological experiments, notably those of Tod (1973) who found that all of the nine specimens tested gave positive reactions with mollusc serum. Stephenson (1965) has commented on the voracious attacks on the slug Deroceras reticulatum.

A detailed study of the life history of this species in Britain has yet to be published. In the present work larvae were only captured in the autumn of 1977, all third instar, and immature adults were found in the other two years, mostly in 1976, in June and July. The adult activity period is very restricted, and reminiscent of Abax parallelepipedus, although unlike that species only single peaks in larvae and immature adults were found. It would appear then that the life cycle can be completed within a year in this species, and that the "type" is Thiele's (1977) second with larval overwintering and late summer breeding. Overwintering was demonstrated in both sexes, although no individuals were found to enter more than two breeding seasons.

8.270 Pterostichus niger

Pterostichus niger is found throughout most of Europe, but is restricted to the north eastern corner of the Iberian Peninsula, and to the southern parts of Scandinavia. The range extends well into Asia (Turin et al, 1977). Like Carabus violaceus and P. madidus, it is a eurytopic species being found in woodlands, grasslands and arable land (Greenslade, 1964c; Neumann, 1971; Evans, 1975; Thiele, 1977).

Thiele (1977) found that individuals spend most of their active period in the litter areas, and often enter open areas of ground. The running speed he found was the highest for its size. Thus, it behaves much as N. brevicollis and C. violaceus in this respect. However, Evans (1977) found it to be a powerful pusher and burrower, and so like P. madidus and A. parallelepipedus. It would appear, therefore, to be a very versatile species.

The species is a general predator and scavenger (Evans, 1967), and practices pre-oral digestion, consuming the liquified food (Davies, 1953; Thiele, 1977). Drift (1951) found chitin remains of arthropod prey in the guts of specimens, and the frequent presence of mollusc remains was demonstrated by Tod (1973).

The life history is essentially similar to that of C. violaceus (Thiele type 2). Larvae are active in October, January, February and May, and adults recently emerged from pupation are present in July and August. Overwintering of adults of both sexes is common. Although scarce in 1976, the species was very common in both 1977 and 1978, and this may be due to the exceptional weather conditions experienced in 1976 (see Chapter 2.500). Details of the life history in a Danish wood are given in Jorum (1980).

8.280 Life Expectancy

8.281 Mortality

Mortality may result from biotic and abiotic factors. Abiotic factors include unfavourable temperature, humidity, and chemicals, and the reactions to these of carabid beetles have been reviewed recently by Thiele (1977). Biotic factors include predation, parasitism, starvation and ageing. A wide range of predators have been described in the literature, and many of these are known to occur in the present study site. Mammals, birds and amphibians are involved as well as invertebrates such as wolf spiders (Lycosidae), centipedes, and ants (Houston, 1970), and also staphylinid beetles (Nield, 1976). Cannibalism is well known in the family under laboratory conditions, as is predation by one species upon another (e.g. Thiele, 1977; Grüm 1967). However, field observations are much less common. Grüm (1967) found that, in a number of species, young individuals were attacked and eaten by the adults in the field. Evisceration of males by females in Carabus spp. at the end of the breeding season is another aspect (see 4.500).

Parasitism is reasonably well studied in the Carabidae (reviewed in Thiele, 1977). Few parasites were recorded from the study site. Of 66 Nebria brevicollis adults dissected three contained parasitic worms (Table 4.3), and of 17 larvae reared in the laboratory, two produced parasitic wasps (Table 4.5). Internal parasites were not found in the other four species. Larvae of all species frequently succumbed to fungal disease under laboratory conditions, but this may be a reflection of poor laboratory methods rather than a common disease in the field. One parasitic mite (species unknown), and

evidence of others, were found to be sucking the body fluids in Pterostichus madidus from positions near the shoulders of the elytra. Other mites observed appeared to be phoretic rather than parasitic.

At first sight, starvation appears to be an unlikely source of mortality under normal conditions. Like most predators, carabids have the capacity for consuming large quantities of food when available, and for surviving long periods without (Grüm, 1966b and 1975). However, recent studies by Houston (1981) have shown that increasing mandible wear with age restricts the suitability of prey items and will lead ultimately to death through starvation - unless the increased foraging activity needed to provide sufficient food intake leads to its own predation.

Ageing processes, other than that of mandible wear, have been little studied in Carabidae.

Grüm (1975) studied the mortality patterns of some carabids in Poland, and found that adult mortality was highest in the breeding season, i.e. the mobile phases are the most susceptible to mortality factors. Other conclusions reached were that : mortality rates do not change according to the age of the individual; mortality changes are not dependent on population density; and weather conditions are not directly effective. He proposed that survival is related to activity levels, to exposure to the predators.

8.282 Longevity

In Chapter 4.8, the results from the individual marking experiments were used to demonstrate the numbers of beetles which survive into more than one breeding season. Survival into a second breeding

season was clearly demonstrated for all five species. In Nebria brevicollis 22% (137) of the marked beetles were active within the study area during a second breeding season (1975 to 1976), but only 5.4% (79) in 1976 - 1977. Figures for Pterostichus madidus during the same years were 2.97% (43) and 4.4% (56), and for Abax parallelepipedus 13.5% (20) and 5.18% (19). Carabus violaceus gave figures of 10.9% (5) from 1976 to 1977, and 2.6% (1) from 1977 to 1978, and Pterostichus niger 4.7% (2) and 3.1% (8) for the same periods. These figures are all very variable, but do demonstrate that an appreciable percentage of these beetles overwinter successfully and enter a second breeding season. It is interesting to note that the figures for Abax are not dramatically different to those of the other species. Since the life cycle requires adult overwintering (see 8.250), a better survival rate might be expected.

In Nebria brevicollis, Pterostichus madidus, and Abax parallelepipedus individuals were also shown to reach a third breeding season : 0.5% (3) Nebria from 1975 to 1977; 0.9% (13) P. madidus from 1975 to 1977, and 0.7% (9) from 1976 to 1978; 4.7% (7) Abax from 1975 - 1977, and 4.1% from 1976 - 1978. Interestingly, survival of Abax beetles into a third season is noticeably much greater than in the other two species. P. madidus and Abax also contained individuals which entered a fourth breeding season : 0.5% (7) and 3.4% (5) from 1975 to 1978 respectively.

The question of age-related mortality can also be investigated using these figures. Of the 22% (137) N. brevicollis which lived from 1975 - 1976 only 2.2% (3) reached the 1977 breeding season. This is a large decrease and may suggest increased mortality with age, but

may equally indicate movement out of the study site in this active species. In both P. madidus and Abax there is an increase rather than decrease: in the P. madidus run from 1975 to 1978 the percentages are 2.97% (43), 30.2% (13) and 53.8% (7); the same species for 1976 - 1978 gives 4.4% (56) and 16.1% (9); Abax from 1975 to 1978 gives 13.5% (20), 35% (7) and 71.4% (5); and, for 1976 to 1978, 5.18% (19) and 78.9% (15). In these two species age clearly is not directly related to survival.

Early ideas concerning the expected life span of a carabid beetle centred around the basic life history: egg to egg-producing adult in little more than one year (mentioned by Thiele, 1977). Studies during the last quarter century have shown this to be true for only a proportion of the population in autumn breeding species. Adult overwintering has been observed in a number of species and, indeed, some life histories require it (e.g. Abax parallelepipedus and A. ovalis). Overwintering has been demonstrated by the presence of mature adults before the emergence of the new generation (Gilbert, 1958; Fairhurst, 1969; Haines, 1973; Nield, 1974), by the presence of dark corpora lutea at the base of ovarioles during egg development (Gilbert, 1955; Barlow, 1970; Kurka, 1972; Dijk, 1973; Heerdt et al, 1976), by examination of mandible wear (Houston, 1970 and 1981) and by marking studies (Tipton, 1960; Schjotz-Christensen, 1965). Heerdt et al (loc.cit.), using an ocular micrometer to measure the size of the corpora lutea in the ovariole bases, have shown that some individuals of Pterostichus oblongopunctatus Fab. enter a third breeding season. However, generally speaking, only marking studies are sufficiently definite to demonstrate beyond doubt the life span possible for beetles in the field.

Thiele (1977) has maintained an Abax parallelepipedus in the laboratory for 3 years 9 mths, and mentions a Carabus auratus, kept by Kern, that survived for five years in captivity. Such examples are, however, not relevant to the hazardous conditions of the field. Schjotz-Christensen (1965) however, found individually marked female Amara infima Duft. which had entered three reproductive periods, Harpalus anxius Duft. beetles which had hibernated on three occasions, and four H. smaragdinus Duft. which had hibernated on four occasions. Vlijm and Dijk (1967) found that about one third of the adult population of Calathus melanocephalus were in their second year. It therefore seems that life spans of more than two years are far from exceptional.

Two studies have found that reproductive activity shortens the life expectancy of the beetles: Burgess and Collins (1915) with Calosoma sycophanta Linn., and Oertel (1924) with Carabus granulatus. However, the present study indicates that there is no such correlation in the five species investigated. Indeed, older individuals appear to persist longer! Dawson (1957), studying Fenland Carabidae also found no evidence for shorter life expectation in individuals which had bred at least once before.

Dijk's studies on Calathus melanocephalus (1972, 1973, 1979) have illustrated the ramifications resultant from the diverse age structure. Females breeding for the second time produced, on average, fewer eggs than the new generation females, and the overwintered individuals are fully mature earlier than the new generation. Since the new generation females mature earlier than the males, matings between old males and young females will precede matings within the new generation of mature

adults.

8.300 Mobility of the different stages in the life cycle

8.310 Larval stages

Larvae of Carabidae are characteristically long-bodied and relatively short-legged. They are therefore poorly adapted for prolonged rapid movement or for sustained mobility. As the main overwintering stage in the life cycle, they are active during the coldest months of the year. These stages are best regarded as primarily feeding stages, and not as a significant dispersal stage.

Burrow-living has been described in the larvae of Nebria brevicollis (Richards, 1946), and pupae were also found in similar, deeper burrows. Similar burrows to those described by Richards were found in the compacted soil of footpaths within Great Wood during May 1976. On investigation, these were found to contain either third larvae instar N. brevicollis or common earwig (Forficula auricularia Linn.) (see Ch. 4.700). One larva was retained and kept in the laboratory where pupation occurred a few days later. Whether or not all larval stages construct such burrows is not clear. It may be that only the third instar larvae construct burrows, perhaps only as a precursor to pupation. Some North American species are known to construct burrows and to forage from them (Kirk, 1972; Alcock, 1976; and see 8.542). The nature of the N. brevicollis burrows indicates some degree of permanence of use, and this is further indication of the relative unimportance of larval stages in the spread of the species within the habitat.

Evans (1969) has found that Abax and Pterostichus larvae show a greater degree of activity within the litter and soil, and much less

surface running than in Carabus and Nebria larvae. Thus, they will tend to produce much smaller nett displacements with time, the medium of their movement being denser. Greenslade (1961) found larval N. brevicollis to be relatively inactive as compared with adults, although they are known to be surface active (Evans, loc. cit.; Penney, 1965; Tipton, 1960). Additionally, Luff (1975) comments that older N. brevicollis larvae are probably more mobile than younger, and so more readily caught, and Houston (1970) suggested that larval surface-running, and hence capture proneness, was greatest when searching for a pupation or hibernation site.

Larval dispersal was not investigated in the present study, largely due to the difficulties involved in giving individually recognisable marks to small animals. Any marks applied would not be permanent either, since moulting would shed them.

8.320 Adult stage

The adult carabid beetle is quite different from the larva in the relative length of the body and legs, being relatively long-legged and short-bodied. This combination is a better adaptation for fast and prolonged movement. This feature, together with the reproductive function, makes this stage the most useful for dispersal.

In addition to pedal mobility, there is the possibility of flight. As mentioned above (8.220) only N. brevicollis and P. niger, of the five species, possess fully-developed wings. However, reports of actual flight are very rare. This is partly due to the fact that optimal conditions for flight, i.e. relatively warm air temperatures and more or less still air conditions, occur only rarely in Britain

(Briggs, 1965), and also to autolysis of the flight musculature. The general picture of flight in Carabidae is that, in species where it is possible, it occurs in early adult life. Many researchers, using a variety of species, have found that the flight musculature of females is only functional prior to ovarian development, the reproductive system expanding into the space formerly occupied by the flight muscles (Tietze, 1963; Houston, 1970; Meijer, 1974; and Carter, 1976). Van Huizen (1977), working with Amara plebeja, considered the autolysis to be only temporary, flight muscles regaining their function after egg-laying had ceased. Jackson (1956) dissected a number of N. brevicollis and found that functional flight musculature was the exception, not the rule. Nelemans (1981) found a similar situation.

A relevant fact here is that the integument of immature adults remains relatively soft for some weeks after pupal eclosion. The beetles are therefore more vulnerable to predation. Frequency of capture and the nett displacement figures (see Ch. 5) indicate relative inactivity during this stage. Thus it would appear that even in those individuals capable of flight, the ability is not, or only rarely, used.

All five species studied are ground-living species, foraging over the ground surface, and escaping from predators, etc, by running and hiding. Flight does not appear to be an essential part of their lives.

8.400 Adult Mobility

8.410 General Introduction

Before any conclusions on the spatial effects of mobility can be drawn, the reasons behind that mobility need to be considered. The underlying neurophysiological "motivation" of mobility is not considered here, nor the detailed behavioural mechanisms involved in the

responses to the habitat; rather the overt, and more simplistic, manifestation. Two basic functions are considered : positive or seeking responses, and negative or avoiding responses. The two are obviously interrelated in that predator avoidance will involve refuge seeking, just as food seeking will involve avoidance of unproductive areas of the habitat. However, the two broadly opposing "motives" are useful concepts for discussion.

The primary seeking objectives are the location and use of food, shelter, mates, and, in the case of females, oviposition sites. Avoidance mobility is mostly the negative aspect of all of the above - avoidance of food shortages, and lack of shelter, mates or oviposition sites. The more immediate avoidance of predators, i.e. detected predators, is a somewhat different case to a general policy of predator-avoidance by remaining in refuges when not actively seeking food, mates, or oviposition sites. More distant motivation, or "planning ahead", is very difficult to demonstrate. The selective advantage of avoiding seasonally unfavourable conditions before they begin by using environmental cues is easy to see, but whether or not long-distance movements are the result of normal food, mate and oviposition site seeking, or of an actual dispersive strategy either internally motivated or related to local conditions, is difficult to demonstrate. This is particularly true where the method of mobility is the same in both cases. Flight in a ground-living species may readily be placed in the category of motivated dispersal, but long distant pedal movement across more or less uniformly suitable habitat is more difficult to separate from daily activities. Movement across uniformly unfavourable habitat, e.g. a woodland species

in grassland, must again not be related to the immediate needs if the woodland conditions are still favourable. Unfortunately, the detection of the more intricate changes within the study site was beyond the scope of this study, and only changes directly related to the climatical seasons could be investigated. A wide variety of influences act upon the individual beetles and these interact to produce the mean displacement and time intervals between captures recorded by the methods used in the study. These two aspects of the recapture results are correlated with gross seasonal changes and gross changes in the reproductive condition and age of the beetles in Chapters 5 and 6. The inherent dynamism of the beetle - habitat system should not be lost sight of. An individual's habitat requirements may change subtly with the internal condition of the beetle, and the sources of fulfillment of those requirements occur and recur at different places and times, and persist over different extents of habitat and durations of time.

Extensive old oak coppice woodland is a particularly stable habitat, changing little in gross terms from year to year. As such, it is a good habitat in which to investigate local mobility. Thiele (1977) and Southwood (1962) consider that stable habitats are characterised by a low "investment in dispersal". If their conclusion is correct, then non-dispersive behaviour of individuals within the population should be much easier to discern.

The existence of migration in the Carabidae has recently been reviewed by Thiele (1977). No evidence has been forthcoming for any of the five species which are the subject of the present investigation. The three main areas for consideration here are (i) dispersal: the

active spread by directed movement, and usually within the species habitat; (ii) drift: the passive spread resulting from random movement; and (iii) local movement within a home range or territory. All three may be involved in the movements of a single individual in its lifetime, and it is one of the aims of this study to seek a pattern of such movements.

Dispersal and drift both result in a shuffling of individuals within the population (population interspersion), whereas home ranging or territoriality do not. Nomadism can involve any of the three ideas, by focussing on temporary centres whose stability depends on the availability of food supply (see 8.500).

The above discussion is a synthesis of the ideas of Elton (1927), Heape (1931), Holt (1955), Andrewartha and Birch (1954), Clark et al (1967), Caughley (1977), and the personal views of the present writer. Baker (1978) was also consulted.

Food-seeking strategies in animals generally have been investigated by a number of authors. A common pattern in active food gathering, as opposed to a sit and wait, purely predatory, strategy, has emerged. The basic tactic is to initiate a random search pattern until a food item is detected, and then, following consumption (or the escape of the prey), an increased turning rate is used to seek other items in the immediate vicinity, before returning to the random search. This pattern has been found in coccinellid beetles (Banks, 1957; and Dixon, 1959), syrphid fly larvae (Chandler, 1969), mites (Fleschner, 1950), anthocorid bugs (Brunner and Burts 1975) and thrushes (Smith, 1974), for example. The theoretical and computer-simulation studies of Hassell are very relevant here (e.g. Hassell et al, 1976

a and b; Hassell and May, 1974), but are beyond the scope of the present work.

Although a "sit and wait" strategy has been observed in Carabidae - Gradwell (1954) reported a Pterostichus madidus adult beetle emerging from beneath a stone, running to a passing earwig, Forficula auricularia, and after immobilising it, carrying it back to its refuge beneath the stone - nocturnal foraging is the more normal activity seen in the five species, as detected by pitfall trapping. The food preferences of each of the five species are described in 8.200.

The food-seeking strategy of Carabidae has been considered by a number of authors. Mitchell (1959), working the day active Trechus quadristriatus and Bembidion lampros, obtained results very similar to those described above for other animals. After encountering a prey item, movements were in the form of small tight turns and were much slower, maximising the chances of encountering neighbouring items. When no further prey items were found the beetles returned to faster movements. Similar results were obtained by Coaker and Williams (1963) working with B. lampros and three other species. Mason (1972) working with Abax parallelepipedus, Pterostichus madidus, Nebria brevicollis and Carabus violaceus, described their foraging activity as exploring the woodland floor surfaces with random movements. More recently, some laboratory studies on P. madidus (Hamilton 1981), have shown that adult beetles of this species aggregate their search for food in regions of high prey density, apparently by means of a change in walking behaviour after feeding. Thus it would appear that foraging strategy in Carabidae is broadly similar to that of other animals. Other recent work is described in Mols (1979), Ernsting et al (1985) and Griffiths et al (1985).

Food recognition is mainly through the contact senses of touch

and taste and the beetle seizes the prey with its mandibles (Thiele, 1977; Evans, 1964, 1975). It may also seize any moving object within reach, and may pursue those not immediately seizable (Gradwell, 1954 and Mason, 1972). The work of Bauer (1982 a, b, and 1985) is also relevant.

The behaviour of a beetle following prey capture also needs consideration. Nett displacement is zero while the beetle consumes the prey, although it may carry the food a short distance to shelter (e.g. Gradwell, 1954). The beetle may not immediately continue its search pattern following consumption. This possibly depends on the relative volume of the prey item, and on the species of beetle. Mitchell (loc. cit.) found that searching continued immediately after consumption, although the food items, eggs of cabbage root fly (Erioischia brassicae Bouche.), are small compared with the volume of the beetle. The strategy of more intensive search of areas producing food items similarly limits the activities of the beetle to a relatively small area. Plotkin (1981) has recently shown that feeding in Pterostichus melanarius produces an increased sensitivity to food items, so that they are more rapidly located and contacted, and he suggests that this may be a non-specific lowering of olfactory thresholds.

The question of sufficiency of food now arises. Ernsting (1977) working with Notiophilus biguttatus found an indication of a hunger threshold below which active searching stops, although capture, eating, and perhaps pursuit, may still occur. Grüm (1971), with various Carabus spp. (but not C. violaceus), similarly found that "hungry" individuals were characterised by high mobility, and that feeding resulted in a decrease in mean mobility. Briggs (1960) also found that activity

in Harpalus rufipes was depressed during the fruiting period of strawberry plants (the beetles were feeding on the fruits) when food was most abundant. With patchy food resources, a good feeding area will result in the tendency to aggregation of the beetles, as mobility decreases within the area as well as net displacement (due to intensification of search) - Grüm (1971), and also reported in Pterostichus madidus, but not Abax parallelepipedus (Frank, 1967c; East, 1974). However, Kulman (1974) found that the availability of prey even over an extended period of time, did not appear to have a consistent effect on carabid populations.

In Calosoma sycophanta, Burgess (1911) found that food intake increases during the breeding season, as would be expected with females producing eggs. Carabidae are able to survive long periods without food (Burgess, loc.cit.; Kabacik et al, 1971), but also to consume large quantities when available (e.g. Abax parallelepipedus, Frank, 1967b; Kabacik et al, 1971; and Scherney, 1959, using Carabus spp. and Pterostichus spp.). This results in a very variable daily consumption. Alcock (1976), working with Dicheirus piceus Mene. larvae in Arizona, reported that one foraging bout may provide sufficient food for a couple of days. Lomnicki (1978) has pointed out that, when food is abundant, differences in food intake between individual animals will be small, but that these differences will increase as food becomes scarcer. It may also be possible that lack of food increasingly produces "stress" of some form, lowering the individual's thresholds of reactions, making it more likely to undertake directed movements in search of food. Baars (1979b) suggested that random movement is characteristic of satiated beetles, whereas directed movement occurs

in hungry individuals; that random walk is the result of frequent encounters with food.

The relationship between food and adult mobility is thus a complex one. However, it is clear that feeding results in relatively low nett displacement.

Just as predation is determined by some internal physiological state ("hunger"), so is reproductive activity. Activity peaks during the breeding season are well known amongst Carabidae (Greenslade, 1961; Evans, 1969, etc.). These peaks also represent feeding activity in females, which are building up their food resources for future egg laying, as well as in males where increased activity in their reproductive system also is occurring (Evans, 1969). The meeting of the sexes happens by chance while the individuals are foraging; however, during the breeding season, there is usually a considerable increase in activity resulting in more encounters between the sexes. Grüm's (1962) studies of the co-occurrence of larvae and adult beetles led him to conclude that the females do not lay the eggs in their normal foraging areas but move to a different woodland habitat for oviposition. A similar situation has been described by Briggs (1965) for Harpalus rufipes where eggs were laid in the weedy areas adjacent to the strawberry field feeding areas. Either the larvae or the young adults must return to the adult feeding areas. In general, however, reproductive strategy has been very little studied in Carabidae and, in consequence, the scattered results do not combine to form a good overall picture, and often are contradictory. It is clear, however, that increased activity is characteristic of both sexes during this

period. Interestingly, Nowak's (1969) studies of Pterostichus niger and P.nigrita suggest differences in the metabolism between the sexes even outside the breeding season, leading to differential food consumption.

Emigration, the movement of individuals out of their normal habitat and across unfavourable habitat, is not considered in this study.

The reactions of the beetles to their population density has been little studied. The recognition senses appear to be the contact ones of touch and taste (Evans, 1969), and so any "density awareness" will result only from the frequency of encounters with other individuals. Under natural conditions it would appear that density-dependent mobility does not occur, or at least, some aggregative response may be present. Mobility has been found to lead to aggregation in optimal sites (Grüm, 1971; and Haines, 1973), but this appears to be a reaction to the optimal conditions rather than to other individuals. A tendency to remain in areas of high density was also found in the present study (see 3.450 and 5.300). The indirect effects of high density resulting in food shortage, will lead to increased mobility, as described above. Brunsting et al (1984) have demonstrated density dependent regulation of numbers in Pterostichus oblongopunctatus, achieved through variation in egg production, larval cannibalism, and adult mortality.

In the present study, pitfall trapping is used to demonstrate the collective effect of the activities and relationships described above, both through the seasons, and from year to year. The results for the individual study species are discussed next.

8.420 Nebria brevicollis

This species is the most active of the five species studied, and lives at relatively high densities and in a highly contagious distribution

over the woodland floor (see 4.200 and 8.230). As such, it is a very useful subject for mobility studies.

Immature adults, initially recognisable by their soft cuticle and, sometimes, paler colouration, are active during May and June. A few examples were found in September, apparently the result of eggs laid late in the season (Luff, 1975; and see 4.200). Although only a few marked individuals were recaptured, these beetles appear to show only low activity levels with little resultant displacement of individuals in space. The duration of their activity is also restricted, being a period of approximately two months between pupal eclosion and the onset of summer aestivation. The relative inactivity of this stage has also been commented upon by a number of other authors (Gilbert, 1968; Greenslade, 1961; and Evans, 1971). This must however be a period of intensive feeding prior to aestivation; and the prey animals (springtails, mites, etc.) will be abundant at this time of year. The low displacement of individuals, therefore, indicates that rapid feeding at a good time of year does not involve directed movement over the woodland floor. Random foraging, producing relatively low displacements, appears to be the picture at this time of year. The abundance of food items will not necessitate directed movements in search of better feeding areas.

With the onset of the summer aestivation period, activity virtually ceases. Only two beetles were pitfalled during the middle of this period, in July 1976. This very limited activity was also found by Ganagarajah (1964) and Anderson (1972), who regarded it as merely a shifting of aestivation site, and hence of restricted movement (4.200).

Activity is resumed in late August and early September, reaching a peak in pitfall catch numbers in October before trailing off again with the onset of winter (4.200). Reproductive activity is confined to this period, as shown by dissection studies (4.200). September is characterised by a high frequency of recapture of marked individuals, although the resulting spatial displacements are relatively low. The mean time period between successive captures in mid September is 3.76 days, and a gradual decrease is seen to a value of 11.85 days in November (see Table 5.15). However, nett displacement of individual beetles steadily increases to reach a peak before catch size begins to fall off (5.352). The mean displacement rate reaches its peak at 10.13m per day in late September. This rate compares favourably with those reported by Tipton (1960) and Greenslade (1961) whose figures, converted to metres per day, are 12.3 and 11.1, respectively. One individual achieved a nett displacement of 90m in one night. Tipton (1960) reported a highest figure of 68.6m in 2 days.

During the autumn activity period, the sex ratio was found to be at its closest to equity (4.200). However, published information on the relative activity of the sexes under field conditions is variable and often contradictory (Tipton, 1960; Penney, 1965; Greenslade, 1965; and Nield, 1974). The relationship between the sex ratio in pitfall traps and the actual sex ratio of the population is not clear, but the variability of published results suggests that the pitfall ratio varies with many factors, and is presumably related to the site characteristics. There is a strong positive correlation between the distribution of the beetles over the trap grid in the spring (non-reproductive period of activity) with that in the autumn (reproductive

period) - $P < 0.001$ for no correlation (5.320). Therefore, the optimal sites for feeding and for oviposition must coincide considerably. No evidence was found for any migration to oviposition sites as suggested by Grüm (1962) for other species.

Multiple recaptures of beetles during this period are more frequent than would be expected from a Poisson Distribution ($P < 0.001$, see Table 5.12). That is, captures are not independent of any previous captures. It would appear that some individuals are very prone to capture. This is unlikely to be the result of any attraction (see 5.340), but more likely related to the feeding strategy (see 8.410). Beetles in a productive area for food probably show random foraging behaviour combined with increased turning rates following food capture. Thus, if a trap is nearby, this beetle is more likely to be captured than a beetle wandering through unproductive habitat. A related feature of the trapping results is the tendency of the beetles to remain in areas of highest adult density - nett displacement is highest in sparsely-populated areas, and lowest in the denser areas (5.360). Mean displacement was found to decrease with increasing total catch during September to November, 1976. This has also been reported by Haines (1973). This feature must also contribute to the multiple recapture result mentioned above. A trap situated in an area of high beetle density will have a high catch total and also regularly recapture the same individuals.

Individuals captured for the first time within the grid do not show a marginal distribution as might be expected ($P < 0.001$), and it therefore appears unlikely that the major source of unmarked beetles

is the surrounding area (5.370). These individuals must consist to a large extent of those which have eluded capture within the grid.

Oviposition has already started before the end of September in some females at least, as shown by the presence of spent individuals (dissections, see 4.200). Dissections have also shown that some females still contain eggs as late as February. Winter oviposition is also indicated by the relatively high catch of females during the winter of 1978. There is, however, no evidence for a higher winter survival of females, as suggested by Nield (1973). The sex ratio of the overwintered population in the following spring suggests otherwise. That egg-laying is prolonged and continuous has been reported by many other authors (Tipton, 1960; Penney, 1965; and Luff, 1975). Thus a proportion of females continue activity after the males have virtually ceased. However, this egg-laying activity is unlikely to be different in nett displacement terms from autumn activity. Critchley (1973) found that eggs were laid at random, in or on the surface of the soil, in this species.

Activity of overwintered beetles resumes in the spring, reaching a peak in March before the new generation of adults have emerged (4.200). Marking results show that this activity peak is entirely separated from that of the new generation, as also found by Gilbert (1958). Thus there is little competition for food between the age groups at this time.

As with the callow adults, these overwintered beetles show a low catch size with little resulting displacement of individuals in space (Fig. 5.7). The reproductive organs of these beetles have not

become active again, dissections show only spent individuals (4.200), as also reported by Gilbert (1958) and Haines (1973). The low catch size at this time of year was also reported by Gilbert (1958) and Evans (1971). These beetles apparently enter the summer aestivation period many weeks prior to the callows. Termination of aestivation is, however, coincidental, beginning in late August just as with the former callows. Thus the duration of summer aestivation is not important, only the timing of its termination. The new generation remain inactive for around two and a half months, whereas the overwintered adults remain so for nearer $3\frac{1}{2}$ or 4 months.

The two age groups behave much the same during the autumn activity peak. The overwintered females are characterised by very dark corpora lutea, the remains of the trophic cells of the previous breeding season being retained in this species (4.200). This distinction gradually becomes obscured as oviposition proceeds. That oviposition can occur in two successive years is clearly shown in dissected females with large numbers of eggs, as well as dark corpora lutea, early in the breeding season.

Overwintered adults, unlike the new generation, do not show the falling off of nett displacement following the autumn peak. Although the activity levels fall off in the same way as the new generation, the older beetles continue to be trapped at locations distant from their release point. Recent studies by Houston (1981) suggest a good reason for this feature of the beetles' behaviour - mandible wear, increasing with age, begins to limit the diversity of food items which can be tackled by the beetles, and so they must search further, and

hence cover more ground, in order to find sufficient food. It is an interesting feature that this "surplus" element of the population is "invested" in dispersal (c.f. den Boer 1970, 1971a, 1971b; Reddingius and den Boer, 1970) - this point will be discussed later (8.450).

The dark corpora lutea of the overwintered females were not separable into age categories by eye, although the work of Heerdt et al (1976) suggests that it may have been possible using optical aids. Only three marked individuals, all male, were shown to be active in a third breeding season. These were of a total of 137 marked beetles known to have successfully overwintered (1975 to 1976) into a second season (2.2% survival). The 137 were the only individuals recaptured of 624 marked prior to the emergence of the 1976 callows. This high percentage reaching the second season (22.2%) is, however, artificially high due to the limited sampling conducted during autumn 1975 and the winter of 1975 and 1976.

8.430 Pterostichus madidus

Pterostichus madidus is another abundant species, with numbers probably exceeding Nebria brevicollis on the study site (5.380). As with N. brevicollis, the distribution of individuals through the site is highly contagious, again probably associated with an uneven distribution of favourable habitat (5.310). The beetles are more heavily built than N. brevicollis, and are adapted more for a life of pushing through soil and litter rather than surface-running (Evans, 1969). The relatively low recapture rate, both of males and females (5.310), may be a reflection of their slower, more powerful, movements.

Immature adults are present on the site during the period May to September, with a peak catch total in August. As the major annual source of new individuals, their low catch totals clearly indicate low activity levels. This is understandable during the earlier weeks of activity when the cuticle is relatively soft, and the beetles are most vulnerable to attack by predators. The relative inactivity of the callow beetles has been commented on by other authors (e.g. Greenslade, 1961).

The reproductive system develops over the summer, a proportion of the females ovipositing in their first season, although some first produce eggs only after overwintering (dissection studies, 4.300, and also reported by Luff, 1973). The recapture results of the marking studies are characterised by a relative lack of displacement in both sexes, with a rate well below 1m per day, the exception being male beetles during August with a figure of 1.94m.per day (5.353). August is also the period of peak activity as shown by catch totals (see above).

The peak displacement rate compares favourably with that calculated by Mason (1972) of 2.43m per day, although sexes and age groups were not analysed separately by this author. Mason's (loc. cit.) study was conducted in, roughly similar, deciduous woodland habitat, and Greenslade (1961) could also detect little movement in his woodland site. However, Greenslade did find an individual (no information on sex or age group) which covered 8.2m per day (figure converted from yards) in grass heath habitat. Nield (1974) reported plenty of intersite movement in garden habitats. Therefore, there appears to be a distinct difference in mobility between woodland litter-living

individuals and those from other habitats.

The relatively high activity, and resultant high displacement rate, of the males falls to a very low level from September through the winter months. During this period female beetles predominate in the pitfall traps (4.300), producing a small peak in monthly catch total in October and November, also reported by Kowalski (1974) and Nield (1974). The peak is the result of increased activity of the females and the predominance of females at this time is not due to relatively high male mortality as suggested by other authors (e.g. Greenslade, 1961). This is clearly seen by the large numbers of overwintered males found during the subsequent breeding season (see 5.353). This peak has been considered to be feeding activity prior to hibernation (Kowalski, loc.cit., and Nield, loc.cit), but it is evidently more than this since male beetles do not show the same behaviour. Dissections of females (Tables 4.8 and 4.9) show that eggs may still be present in October and November, and even in March and May. Just as in Nebria brevicollis, oviposition continues during the winter months. The relative lack of food items during these months, and need for activity in order to oviposit, result in extra foraging efforts. The peak in nett displacement rate is associated with this time : 1.08m per day in November, more than double the July-August figure of 0.41m per day (Table 5.21).

Overwintering is commonplace in this species (4.300 and 5.353) and the reproductive organs of those individuals which had bred in the previous year become productive again (Luff, 1973). Greenslade (1965) has suggested that overwintering mortality is higher in spent

individuals than in those which have not previously bred. Although this was not investigated specifically in the present study, dissection and marking results appear to indicate otherwise. Breeding in a second season is clearly common (5.353), and some individuals even survive into a third, and even a fourth season of breeding activity (4.820). Luff (1973) considered that probably about one quarter of females overwintered and became productive again, and Kowalski (1974) similarly considered overwintering of females commoner than males. The present marking study demonstrated the presence of 13 beetles, including four males, during their third breeding season in 1977 (0.90% of the 1448 marked prior to the callow emergence in 1976); and a further seven individuals, including three males, were found in their fourth season in 1978. The 1978 season also produced nine beetles, four male, which were clearly in their third season following their first trapping in the 1976 season (0.71% of the beetles marked at that time).

The majority of females lose the corpora lutea before the onset of the second breeding season, a feature also reported by Luff (1973) in this species, and in other Pterostichus spp. by Dawson (1957). Thus aging of dissected females by this method is not possible.

As with the new generation beetles, recapture results of overwintered beetles are again characterised by a relative lack of nett displacement in both sexes. Male beetles again provide the exception, but their peak in activity (registered by pitfall trapping) and in nett displacement rate occurs during June and July, and was found to be distinct from that of the new generation males' peak in August,

(5.353, and Fig. 5.15). This has also been reported in Calathus melanocephalus, where the main period of reproductive activities of the two generations also occur in different parts of the breeding season (Dijk, 1973).

The peak displacement rate found was 3.17m per day during July, (Table 5.21), and was the highest recorded for this species and is more than half as much again as that recorded for new generation males. Therefore, as with Nebria brevicollis, the older males tend to produce the higher nett displacements, although there was no evidence in P. madidus of a prolongation of this feature outside the breeding season activity peak.

Grüm's (1962) suggestion of an oviposition migration (for other species) was also investigated for this species (5.320). A correlation test for the distribution of trapped beetles early in the season (when oviposition is at a low level) and during the peak period of breeding activity produced a probability value of approximately 0.05, and so no evidence was obtained of an oviposition migration. Indeed, nett displacement figures show the females to be the least active of the two sexes. Comparison of the frequency of recapture distribution (5.340) with the recapture results (5.353) also shows a tendency for female beetles to have a very limited area of activity. Too many multiple recaptures were found for the frequency distribution to be equivalent to a Poisson Distribution ($P < 0.001$ in females, as compared with $0.70 > P > 0.50$ in male beetles). Although the explanation for this high number of multiple recaptures was sought in high activity levels and the contagious distribution in Nebria brevicollis (sexes not separated), such an explanation does not fit

for P. madidus. As the recaptures were predominantly in the same traps (5.353), the results are perhaps more suggestive of site attachment although as pointed out for N. brevicollis (8.420), foraging in a productive area which also contains a pitfall trap will result in a high probability of capture.

As with N. brevicollis, displacements which were detected tended to be larger in areas of low catch size, and smallest in areas of high catch size (5.362). Thus, only suboptimal or unfavourable locations were characterised by a tendency for greater displacements of individuals.

The source of unmarked beetles within the study grid was also investigated (5.370), but no correlation of their distribution with that of the marked beetles was demonstrated. Unmarked beetles were, however, regularly captured in the centre of the grid and, since marking studies have shown a very low nett displacement rate in this species, it seems likely that a high proportion of the unmarked beetles are merely those resident beetles which had not previously been captured.

The most interesting feature of this species is the apparent maintenance of location. Only during the breeding season do males, and males alone, wander any great distance from the vicinity of the trap where the beetle was originally captured. Unfortunately, previous research on the mobility of this species has not separated the results according to sex or age group.

There are two alternative explanations for this apparent location maintenance. Firstly, this species is omnivorous, taking a wide range

of food items, perhaps necessitating less movement to reach satiation. N. brevicollis feeds on small, very active, prey items such as springtails and linyphiid spiders, and will therefore need to be a fast hunter and to consume large numbers of items in order to reach satiation. The alternative to this "passive" explanation, is an "active" one wherein the beetles actively maintain their location in the habitat, akin to home ranging, and perhaps associated with the location of their daytime refuges. This latter explanation will be discussed in detail later (8.500).

8.440 Other species

8.441 Introduction

Pitfall catch size and recapture rate for Abax parallelepipedus, Carabus violaceus and Pterostichus niger were considerably lower than for Nebria brevicollis and Pterostichus madidus, reflecting much lower population densities. The best results were obtained with Abax, but the complexity of the life history necessitates many more recaptures before detailed mobility analysis is statistically possible. Mobility studies are further hampered in all three species by the restricted annual activity periods. In effect, the results achieved for all three species are too few for analysis comparable to that for N. brevicollis and P. madidus. A few comments are possible, and these are included below.

8.442 Abax parallelepipedus

The broad and ponderous form of this species (Thiele, 1977), together with its powerful "wedge-pushing" abilities (Evans, 1977), are indicative of its life style of moving through the leaf litter and soil in search of a wide variety of food, both living and dead

(Davies, 1953). It was suggested in 8.430 above that the similar, although less powerful, P. madidus, with a similarly omnivorous diet, will need to forage less and hence cover less ground than the very active N. brevicollis in order to reach food satiation. It might be expected then that Abax will exhibit only low displacements with time in the study grid. This is, in fact, what was found (5.354). The largest displacements occurred mostly early in the activity season, and were mostly male beetles (Fig. 5.18). However, only small numbers of beetles were recaptured. Mason (1972), working with a larger population, found the opposite to be the case, that displacement rate increased with the progression of the season. Greenslade (1961) suggested that the low recapture rate experienced was related to extensive dispersal of the marked beetles; however, displacement results do not bear this out.

As with all five species studied, Abax was found to have an aggregated distribution across the study site (5.320), and this again appeared to be maintained by individuals in areas with high catch totals producing the lowest displacement rates, and vice versa (5.362) - a feature also reported in this species by Haines (1973).

Abax parallelepipedus was the only species of the five where a significant difference in recapture rate was found between the sexes, males apparently being recaptured in higher numbers than females. This must be related to the higher displacements achieved by males described above, but why a similar result was not obtained in P. madidus, where the sexes more clearly behave differently, is not clear.

8.443 Carabus violaceus

This is the largest of the five examined in the present study, but is of slender form and long-legged, with an agile and very active life style (Lindroth, 1974). Although omnivorous, it is a voracious predator (Davies, 1953; Stephenson, 1965). Such a large, mobile beetle might be expected to produce a relatively high recapture rate and evidence of large displacements, but this was not found to be the case. The few recaptures obtained (5.355) are suggestive of a higher displacement rate in the female beetles than in males, but large displacements were not, however, found.

8.444 Pterostichus niger

This is another general predator and scavenger (e.g. Evans, 1967) and, like Carabus violaceus, a fast runner (Thiele, 1977). Few recaptures were made during this part of the study and, as with C. violaceus, a higher displacement rate was found in the one female recaptured than in the few males.

The mobility of this species has been studied extensively by Grüm (e.g. 1965), but the poor results of the present study do not merit comparison.

8.450 Discussion and Conclusions

Mobility, whether for feeding or reproductive purposes, can be considered to consist of three main elements:- frequency of turning, angle of turning, and speed of motion. If frequency and angle are both high, then relatively low nett displacement will result, e.g. when foraging in a rewarding area. When both are low, high nett displacement will occur, and speed is especially important, e.g.

when searching for new and improved feeding areas. When frequency and angle are random, then, again, relatively low nett displacement will result (see Skellam, 1952). It is the balance between these three aspects which determines the length and speed of nett displacements observed by pitfall-trapping, and which, it is thought, characterises the differences between the individual beetles - differences between sexes, age groups, and the individual beetles themselves. The present investigation has revealed some of these patterns of mobility in the species studied.

The different patterns of behaviour between N. brevicollis and P. madidus reflect, to some extent, their different lifestyles. N. brevicollis, an active predator with a somewhat specialist diet, produced the highest capture frequencies and the largest recorded nett displacements. The omnivorous P. madidus produced both lower capture frequencies and smaller nett displacements. With a wider choice of food items, the chances of the latter species of encountering prey will be relatively greater, and so it should not need to travel so far to achieve satiety. This species is also anatomically adapted to hunting in enclosed spaces, such as within leaf litter (Evans, 1977) and it will therefore be slowed by the density of the medium in which it is active. The detail of the results, however, shows that much more is happening than this simple picture supposes.

In N. brevicollis, the results of the present investigations tie in very closely with those of other workers. A very straightforward picture emerges, with the higher nett displacements associated with the onset of reproductive activity, and areas of relatively poor quality habitat, where the food- and mate-seeking behaviour is not

being rewarded sufficiently (areas of lowest adult density). Lower nett displacements are, conversely, associated with areas rich in food and mates, and including periods of rapid feeding before and after the midsummer aestivation period, and with sexually immature individuals. A complication is introduced by the difference between individuals in their second breeding season and those in their first, whereby the relatively high nett displacements do not decrease with the onset of winter in the second season individuals. This point will be returned to later (8.500).

In P. madidus, sexually immature individuals are similarly characterized by relatively low nett displacements. However, this is also the case in mature individuals, the only exception being male beetles during the main period of reproductive activity - in June and July for beetles in their second breeding season, but in August for the new generation of males. Female beetles only show a slight increase in activity, from September onwards, probably associated with oviposition. Greatest nett displacements are seen in the male beetles during their second breeding season. Since no firm evidence for home-ranging has been found, the relative lack of nett displacement resulting from feeding activity is probably due to the omnivorous habits of this species making less foraging necessary.

The two species differ in that the main period of reproductive activity of the age groups concur in N. brevicollis, but are clearly separated in male P. madidus. The significance of this is not clear. However, the males which breed earlier in the year are those which have already successfully overwintered, the weaker individuals having

been weeded out of that generation by the poor conditions experienced during the winter months. The later breeding, newly-emerged generation of beetles will include individuals which will not survive the following winter. The different breeding periods may therefore be related to genetic selection, producing individuals better able to survive the conditions of winter. If this is not the true reason for this feature, then it is certainly an important by-product. Dijk (1979) has similarly suggested that the heterogeneity of age structure in other carabid species may enhance the populations stability under the extant environmental conditions.

It is also of interest to note that in both species the older, perhaps more "experienced", individuals produce the larger nett displacements. In P. madidus, this was only noted with male beetles, and there was no evidence for its prolongation outside of the period of peak reproductive activity. With N. brevicollis, both sexes are apparently involved (see 7.210), and the larger displacements continue to be found when the new generation's activity is beginning to fall off.

Recent work by Houston (1981) is very relevant here. His studies have shown that mandible wear and claw wear, not surprisingly, increase with age, and has used this feature to distinguish age categories of the Carabus spp. beetles investigated. Individuals with very worn mandibles and claws may have difficulty in catching and chewing prey items, and dissections (Houston, loc.cit.) have found that such beetles have little or no fat reserves and possess very small and translucent ovaries. The condition is reversed by feeding with macerated rabbit liver, and egg production again becomes possible. The poor condition

of these beetles, therefore, appears to be due to lack of food rather than any general ageing degenerative process. Houston suggests that this inability to utilise the usual range of prey items may account for higher mobility in older individuals - they will need to search more extensively in order to find sufficient prey items of their more restricted requirements. He also refers to studies by Grüm (1979) which show that individual carabid beetles in their second breeding season expend more energy on mobility than the new breeding individuals.

Mandible wear, and the resultant extra food-seeking mobility is, therefore, a strong explanation for the observations on N. brevicollis and P. madidus made during the present study. No other explanation has been forthcoming, although the effects of this increased mobility in the older, and perhaps surplus, individuals of the population on the intermixing and dispersal of the beetles are also interesting to consider.

High nett displacements, by bringing the individuals concerned into new areas of habitat, should result in a greater mixing of the population, and hence a greater mixing of the genetic material. The strategy could be to maintain the local populations first, and only to invest "surplus" beetles in the uncertainties of movement into the surrounding area, where encounters with other individuals of the same species may or may not result. The straying individuals are those whose genetic material have been used over two breeding seasons; they are the beetles which have a proven ability to survive in the immediate environment, and so are more likely to survive to encounter individuals living in the surrounding areas. Their genes are well-represented in the "home" population, and their survival abilities are

more useful to the species if they are introduced to and mixed with other populations.

Whether such an altruistic interpretation is valid or not, this feature of the results clearly merits further experimental investigation. Houston (1981) has shown that beetles can be separated into age categories without injuring or killing the individuals, and so the potential for such a study is much greater. The project would be very long term if individual marking techniques were the only way of identifying the older individuals.

The reason why relatively large nett displacements were found only in male beetles of P. madidus, but in both sexes in N. brevicollis, is another intriguing problem. If only male beetles wander then the spread of the species cannot be involved, only increased mixing of genetic material. However, it may be that different strategies are involved in the two species, and that the potential colonisation of new areas is only implicit in that of N. brevicollis. P. madidus is almost ubiquitous in habitat (8.240), certainly more so than N. brevicollis, and so populations are less likely to be geographically isolated. The movement of both sexes into new areas is therefore not especially desirable genetically.

Interpretation of the results from the other three species investigated is difficult with so few recaptures. The largest nett displacements with time in Abax parallelepipedus were associated with male beetles early in the activity period. This is contradictory to the findings of Mason (1972), who found the largest displacements late in the activity season. Relatively large displacements were not

found in Carabus violaceus, although female beetles produced higher displacement rates than males. Very few recaptures of Pterostichus niger were made. With the paucity of information, further analysis of the behaviour of these species is not feasible.

Pitfall trapping results show the relationship between time and distance at a point of interruption in the activity of the individual beetles, i.e. when they fall into the trap. The methods of Baars (1979b) show the same relationship, but do not involve an interruption of the individual beetle's daily activity, although dramatically decrease the longevity of the beetles used - reducing it to weeks rather than years. The results of tracking radioactively-labelled individuals do, however, provide valuable information on the short term mobility patterns of individual beetles, and offer valuable insights into what might be occurring in the species used in the present study.

Both species studied by Baars (loc.cit.) - Pterostichus versicolor Sturm and Calathus melanocephalus, in heathland habitats - showed periods of small distances covered per day in random directions, alternating with periods of directed movement with large distances covered per day. He could detect no differences in this behaviour between periods of reproductive and non-reproductive activity, or with immature, mature, or spent beetles; or with male or female. In unfavourable habitat directed movement was more frequent and more extreme.

Baars (loc.cit) compared his results with those of Grüm (1965, 1971) who recognised fast-moving and slow-moving individuals and attributed these differences to hungry and satiated individuals res-

pectively. Baars concludes that "directed walk" is an evolved reaction to insufficient prey density, making it less likely that the beetle will return to areas previously foraged over. "Random walk" is the result of frequent encounters with food, probably clustered, leading to only small displacements in random directions. The studies of Ericson (1978) on a population of Pterostichus cupreus Linn. in an agricultural field are also relevant here. The results suggested that the population seemed to consist of both more local individuals, penetrating a limited area, and individuals with a higher, straighter, run mobility. Rijnsdorp (1980) found similar behaviour in Carabus problematicus. See also Griffiths et al (1985).

In many ways, the conclusions of Baars, are readily applicable to results of the present study, although "directed walk" is more associated with reproductive activity in N. brevicollis and P. madidus. Of course, woodland leaf litter is a particular rich food source for these animals, and food will not be difficult to find over much of the growing season. However, the present study did suggest that the aggregated distributions of beetles observed is related to an active process, resulting from the avoidance by beetles of areas less rewarding in terms of food, mates, and probably shelter, also. It is possible that the relatively high activity within the population during the reproductive season results in local food shortages, and so stimulates "directed walk" behaviour in individuals. However, reproduction is linked to the most productive season for the food items of the respective species, and so this proposition seems unlikely. Aggregation areas appear to be stable over the annual cycle, and this also adds weight to the idea that these are especially favourable areas for food items, and that they are not seriously depleted other than by the

annual seasonal cycle. Den Boer (1971a) commented that there was no convincing evidence to indicate that, in populations of carabid beetles, dispersal will be the result of too high densities.

8.500 Spatial Strategy

8.510 Introduction

A wide spectrum of spatial strategy has been described in mobile animals, from true nomadism, where the individual's day to day activities are not related to a particular area or areas within its habitat, to refuging (Hamilton and Watt, 1970), where one or more fixed areas or locations are regularly used by the same individual or individuals, and where these sites may be defended from other individuals (territoriality) (e.g. Heape, 1931; Brown and Orians, 1970; Burt, 1943).

The results of the present study seem to show that both nomadism and refuging, as defined above, are behavioural features of the woodland Carabidae studied. The term "refuging" is used here in preference to "home ranging" in order to avoid the confusion of definition which is apparent in the home range literature. The most widely accepted definition of home range is that given by Burt (1943): "Home range then is the area, usually around a home site, over which the animal normally travels in search of food. Every kind of mammal may be said to have a home range, stationary or shifting." Thus a fixed "home" location, or refuge, is not implicit in the definition, although the term "home range" is often taken in that sense. Jewell (1966) has introduced a further term, "lifetime range", to mean "the total area with which an animal has become familiar, including seasonal home ranges, excursions for mating, and routes of movement", restating

Burt's (loc.cit.) ideas in the form that "home range is the area over which an animal normally travels in pursuit of its routine activities". Even Jewell's useful concept of lifetime range, however, has "familiar" in its definition, implying the regular use of the range, and therefore excludes true nomadism wherein any regularity of use of a particular area is accidental. Refuging, the rhythmical dispersal of groups of animals from and their return to a fixed point in space (Hamilton and Watt, 1970) is, therefore, the best opposite position to nomadism as a concept. "Lifetime range" and "home range" are best regarded as combinations of, and variations on, the basic theme.

8.520 Nomadism

Nomadism, as defined here, is the free movement of individual animals, with no neurophysiological "barrier" of remaining within "familiar" areas, or of extending these "familiar" areas. The individual's habitat preference is the only "barrier" recognised. Species exhibiting this type of behaviour will lay their eggs, or give birth to their young, at random, although in suitable situations, within the habitat, and will use whatever refugia are locally available or necessary for periods of inactivity.

This lifestyle description fits the experimental results for Nebria brevicollis very well, but the restricted activity and small detected displacements of Pterostichus madidus (apart from male beetles during the breeding season) suggest that nomadism may not be the case in this species. However, experimental displacement results did not conflict with the idea of nomadism in P. madidus (see below).

8.530 Refuging

The rhythmical dispersal of groups of animals from, and their

return to, a fixed point in space (Hamilton and Watt, 1970) is a strategy that has been used by animals for a number of basic reasons. The most frequent reasons appear to be (i) the refuge is a safe place for the individual where it is relatively protected from predation, adverse weather conditions, etc, (ii) care of offspring, where the refuge is the nest site, or some other place where the young remain while the parent is foraging, (iii) the refuge is also a food store, where surplus food is stored for future needs, and (iv) the efficient use of food resources in social groups.

In (i), (ii) and (iii) above, the refuge is generally a construction of some sort. Constructions can involve substantial time and effort on the part of the individual and so are unlikely to be intended only for casual or occasional use. Intended regularity of use is clear in the case of brood or food store care (ii and iii), but less so in (i) except where the refuge is a chamber for moulting or pupation, and hence intended for continuous use for a period of time. The efficient use of food resources (iv) refers to social animals such as communally roosting birds, and certain Hymenoptera Aculeata, where the behaviour of the individual animals is far more complicated than indicated here. These animals are beyond the scope of the present discussion.

As long as the daily requirements of the individual are fulfilled by foraging expeditions the refuge may continue to be used, but if the surrounding area becomes sub-optimal, then the individual which is using the refuge purely for self-preservation can seek further afield for a new area and establish a new refuge (e.g. Jewell, 1966; Brown, 1962; Brown and Orians, 1970). Refuges with a food store may be an

adaptation to avoid this necessity.

Inherent in the concept of refuging is the ability of the individual animal to relocate the refuge when returning from foraging expeditions. This implies either familiarity with the immediate environs of the refuge, or some other navigational ability.

8.540 The Study of Spatial Strategy

8.541 Introduction

Published studies of spatial strategy are dominated by work on mammals and birds, where home range and territory, respectively, are the main interest. Experimental studies on invertebrates are thinly scattered in the literature, and a nomadic way of life is generally assumed wherever no conflicting evidence has appeared. Social insects, such as certain Hymenoptera Aculeata and Isoptera, have been the focus of much attention, and studies on territorial behaviour cover a wide spread of insect groups e.g. cicada wasps (Hym., Sphecidae) (Lin, 1963), crickets (Orth., Gryllidae) (Alexander, 1961), and dragonflies (Odonata) (Moore, 1957). In these latter cases, territorial defence is related to courtship area, a nest with brood, or stored food, but not a foraging area (Brown and Orians, 1970). Interestingly, some non-territorial grasshoppers (Orth., Acrididae) studied by Clark (1962) have been found to actively maintain their location within the vegetation, and not drift within the habitat. Grum (1981) has used the mammalogists' home range study techniques to estimate the extent of habitat that a carabid moves within during one season.

An awareness of location in respect to the features of the habitat is inherent in the territorial insects. The Social Hymenoptera need to be able to relocate the nest when returning from foraging expeditions. Similarly, the more or less solitary-living mining bees and wasps (also Hymenoptera Aculeata) excavate burrows or modify natural

holes for their larvae, and forage from them in order to provide a food store for the developing larvae. Again a memory of the site of the burrow in relation to the bee's own position is essential.

"Wandering" spiders invite comparison with the ground beetles. Some Lycosidae, Clubionidae, Gnaphosidae and other spiders move actively over the ground surface, running down or pouncing on their prey, rather than relying on the use of webs (Uetz and Unzicker, 1976; Huhta, 1971; Breymeyer, 1966a; etc.). The wolf spiders (Lycosidae) are particularly comparable, the species being of similar size to N. brevicollis and P. madidus, and active carnivores, moving across the ground with sufficient momentum to fall into pitfall traps (Williams, 1962). However, as with Carabidae, any awareness of the individual spider of its position in relation to the physical components of the habitat has been little investigated. Hallander's (1967) study involving marked Pardosa spp. wolf spiders is of significance, although the basic assumption of a nomadic way of life is inherent in the methods applied (field release points bear no relation to the capture points). Recapture results showed a direct relationship between time and distance at the point of recapture, i.e. continuous movement away from the release point was found. Interestingly, in Pardosa pullata Clerck. the habitat offers good opportunities for food and shelter, and hence shorter distances are covered by individuals, as compared with other Pardosa spp. and also the male spiders need to seek out the females for mating and so move greater distances than the females.

8.542 Refuging behaviour in Carabidae

An important consideration in any discussion of refuging behaviour is the adaptiveness of such behaviour, i.e. what advantage the individual

has in possessing a refuge. In the woodland Carabidae investigated in the present study, the need for a refuge is not readily clear. The leaf-litter and deadwood-strewn woodland floor appears to offer a wealth of suitable refuges. However, scattered through the literature are a variety of comments and observations which shed some light on the interpretation of refuging behaviour in Carabidae.

The larvae of certain North American seed-feeding Carabidae are well-known to maintain a store of seeds in a burrow, from which they forage for further seeds (Kirk, 1972; and Alcock, 1976), and similar behaviour has recently been described in Harpalus rufipes in Britain (Luff, 1980). Burrow-living has already been mentioned in Nebria brevicollis (4.700 and 8.310), where it is suspected that the construction of regularly used burrows is a precursor to pupation, and may not be a feature of the lives of the earlier larval instars.

Burrow excavation has also been reported in adult Carabidae, both under field conditions (Cole, 1946; Kirk, 1972; and Mason, 1972) and in the laboratory (Frank, 1966; Mason, loc.cit.; and present study). These are short burrows, excavated beneath stones, logs, and other solid objects, in which the animals were found quiescent during the daylight hours. Both Mason and Frank (loc.cit.) were studying Abax parallelepipedus and Pterostichus madidus. Hlavac (1967) has found that Scarites sp. adults burrow into the substrate down the side of solid objects, and that captured food was taken into the burrow for consumption. Resting within a burrow, with the jaws pointing towards the entrance hole, is a very good defensive position!

Mason (loc.cit.) commented that the burrows appeared to be regularly

used. The regular use of stones as a daytime refuge by certain Carabus violaceus and Pterostichus madidus was mentioned in Chapter 1, and Manley (1971) found that larvae of Synuchus impunctatus (Say.) retired to the same "home" log as a retreat even if other logs were available for use. Some casual log sampling in woods (other than Great Wood) in the vicinity of Royal Holloway College (see 2.110) however, indicated a transitory use by both male and female P. madidus and A. parallelepipedus.

Location memory - an awareness of the individual beetles of its position in relation to the features of its habitat - is clearly demonstrated in the regular use of refuges by individual beetles. Further evidence of this is seen in comments by Parry (1979) on the behaviour of Laemostenus terricola, where the beetles "ran to the walls of the stone building for shelter on disturbance, and moreover seemed to follow well-remembered paths giving access to deep cavities."

It is clear, therefore, that some species of Carabidae do have the ability to return to particular localities within their habitats and to maintain and regularly use refuges. Whether one or more refuges per individual are involved presumably depends on their availability, and the activity ranges of the refuging individuals presumably overlap considerably.

The suggestion that some form of refuging behaviour occurs in the species investigated in this study is the result of two observations: (i) the persistence of certain individual beetles in small areas of habitat for long periods of time, particularly in Pterostichus madidus, and seen in the regular capture of individual beetles at single trap points (5.353), and (ii) the frequency of multiple recaptures

of individual beetles generally (5.340). Multiple recaptures were also a feature of the trapping results made by Nelson (1970) using Pasimachus punctulatus, and similarly led him to the suggestion that some beetles at least were maintaining an activity centre, and perhaps a home range.

The possibility of refuging behaviour was investigated by concentrating the trapping effort onto an area which had previously produced good numbers of P. madidus (the most suggestive species), and looking at the results of varying the distance of the release point from the source trap. It was supposed that refuging beetles released at relatively short distances from the source trap would still be within "familiar" habitat and so be more likely to be retrapped back at the source trap than elsewhere; alternatively, those released at relatively large distances would be moved to "unfamiliar" habitat, and either react to this stress by wandering large distances in search of the "familiar" area and its refuge(s), or else establish a new one. The results of the displacement experiment in fact showed no evidence of any effect whatever, indicating that the beetles were behaving much the same wherever they were released. It would appear that the distinction between "familiar" and "unfamiliar" areas of habitat does not exist in these beetles.

Regular capture of certain individual beetles at certain individual trap points, and multiple recaptures generally, are now thought to be the result of a trap position coinciding with an area of habitat particularly favourable to the species in terms of food, shelter, mates, etc, and hence having a concentrating or aggregating effect on the beetles (see 8.450). It is particularly striking that in the least

mobile species, P. madidus, the smaller trap intervals of 5m used in Chapter 6 resulted in a greater nett displacement rate than found using 15m intervals in Chapter 5.

The work of Baars (1979) with the nocturnally active Calathus melanocephalus in heathland habitats has shown the relative unimportance of a regular refuge in this species : on successive days individual beetles were often found quiescent at points very close together, but not coinciding, i.e. suitable daytime refuges were abundant and the beetles did not search out particularly suitable ones.

A study of the usage, by individually marked beetles, of natural refuges over a period of years would be an interesting follow-up project. Daytime refugia were difficult to locate in Great Wood, searching beneath logs and amongst litter producing very few beetles and much habitat disturbance. However, in woodland with widely-scattered and frequent stones or rocks, natural refuge sampling could be a viable approach. The methods used by Baars (1979) are very informative, although the induced high mortality rate is a severe limitation.

8.600 Dispersive Behaviour of Carabidae : General Conclusions

The main aim of this study was to investigate the dispersive behaviour of woodland leaf-litter inhabiting carabid beetles, in relation to their life cycles, habitats, and population density. Although the results of the experimental studies were not as clear-cut as would be hoped, some interesting features of the habits of these beetles have been disclosed. Detailed analysis of the results was mainly restricted to Nebria brevicollis and Pterostichus madidus. However, the results from the other three species examined suggest that

similar considerations apply to their dispersive behaviour, differences being in degree or emphasis rather than contradictory.

All five species show active foraging behaviour over the woodland floor, and differences in pitfall catches reflect amongst other things, food availability and reproductive activity. At the termination of activity periods, refuges are sought as protection from environmental hazards.

Large displacements of individuals with time are the result of directed mobility, and are associated with reproductive activity - both sexes in Nebria brevicollis, but mainly male beetles in Pterostichus madidus, and with relatively poor quality habitat - producing relatively poor rewards from foraging activity. Smaller displacements of individuals are associated with random foraging in productive habitat. The slower, more powerful, movements of P. madidus, together with its omnivorous habits, result in generally lower nett displacement than that recorded for N. brevicollis. In female P. madidus, particularly, the results suggest only very limited areas of activity for each individual, and superficially resemble refuging behaviour.

The nett effect of the two extreme behaviour patterns of directed movement in relatively unfavourable habitat and random movement in relatively favourable habitat is to concentrate or aggregate the beetles into the particularly favourable patches of habitat scattered across the site.

Increased mobility is a feature of older beetles, and probably is directly related to mandible and claw wear limiting the range of prey items which can be successfully overpowered and eaten. The foraging

effort needed to achieve satiety will increase with mandible and claw wear, ultimately to a point where death through starvation occurs.

In conclusion, the beetles appear to be best regarded as nomads, moving through the ground litter habitats in search of food and mates, and using whatever daytime refuges are available as required. Each species will occupy its available continuum of suitable habitat, aggregating in optimal areas of habitat as a result of the particular foraging strategy rather than any attraction between individual beetles. Where the area of available habitat is relatively small only relatively small displacements of beetles will occur (e.g. Nebria brevicollis in the small copse studied by Greenslade, 1961), but in more extensive habitat larger movements will be possible (e.g. N. brevicollis in Great Wood). Movements away from favourable sites will result from changes in the environment or internal changes altering the requirements of the individual beetles.

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APPENDICES

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APPENDIX 2.1

Appendix 2.1: Monthly maxima and minima of air temperature recorded in Great Wood, December 1975 until August 1976 (°C).

	1975/76		1976/77		1977/78	
	Min	Max	Min	Max	Min	Max
Dec	-6	9	-4	8	-1½	14
Jan	-3	11½	-3½	12½	-3½	8½
Feb	-1½	12½	-2	10	-6½	11½
Mar	-2½	15	0	15½	-1	15
Apr	-1	18½	-2	17	-1	17½
May	0	26	1½	22½	3½	23½
Jun	8½	29	5	22	7	25
Jly	10	29½	8	25	8	22
Aug	7	26½	7	22	11½	17½
Sept	7	20½	6	19		
Oct	4½	17	4	17		
Nov	-1	11½	4	15		

Number of days when temperature exceeded 25°C

	1976	1977	1978
May	1	0	0
June	9	0	1
July	19	1	-
August	7	0	-

Appendix 5.1(i): Recapture records for *Nebria brevicollis* adults known
known to have overwintered 1975-76

(Abbreviations are as follows: DRC date of recapture; DRL date of last release; IM individual code mark; SRL site of release; SRC site of recapture; d distance between traps (m.); t time interval between captures (days); PRC number of previous recaptures. * refers to those catches where the beetles were not removed from the traps on the day following capture, and so the time interval cannot be determined).

DRC	DRL	IM	SRL	SRC	d	t	PRC
12.iii	10.iii	286	A1	A1	-	2	1
15.iii	12.iii	300	G6	G6	-	*	0
18.iii	16.iii	318	A6	A6	-	2	0
18.iii	17.iii	341	G10	G10	-	1	0
19.iii	18.iii	352	B6	B6	-	1	0
22.iii	18.iii	351	B6	B6	-	*	0
25.iii	18.iii	318	A6	A6	-	7	1
25.iii	11.iii	293	E6	F7	21	14	0
26.iii	25.iii	380	A2	A2	-	1	0
26.iii	25.iii	387	C6	C6	-	1	0
26.iii	25.iii	270	C6	C6	-	1	1
26.iii	24.iii	379	G5	G6	15	2	0
26.iii	25.iii	405	G6	G6	-	1	0
29.iii	18.iii	355	C7	C7	-	*	0
29.iii	26.iii	418	E6	E6	-	*	0
29.iii	26.iii	405	G6	G6	-	*	1
30.iii	18.iii	347	A5	B6	21	12	0
31.iii	25.iii	383	A7	C5	42	6	0
31.iii	26.iii	430	G9	G9	-	5	0
1.iv	30.iii	464	F6	F6	-	2	0
2.iv	1.iv	464	F6	F6	-	1	1
2.iv	26.iii	427	G6	F6	15	7	0
2.iv	18.iii	358	F6	G7	21	15	0
5.iv	2.iv	464	F6	F6	-	*	2
5.iv	25.iii	402	G2	G2	-	*	0
7.iv	16.iii	323	E6	B7	47	22	0
8.iv	7.iv	527	E4	E4	-	1	0
12.iv	6.iv	522	E4	E4	-	*	0
14.iv	25.iii	318	A6	C6	30	20	2
14.iv	26.iii	421	E8	E8	-	19	0
6.v	5.v	629	B7	B7	-	1	0
10.v	7.v	641	A5	A5	-	*	0
20.ix	17.ix	259	A5	A5	-	*	1
20.ix	16.ix	436	C6	C7	15	*	2
21.ix	16.ix	509	G4	G4	-	*	1
24.ix	17.ix	284	G4	D4	45	*	1

Appendix 5.1(i): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
24.ix	15.ix	522	F3	E4	21	*	2
24.ix	17.ix	212	E5	E4	15	7	2
25.ix	16.ix	332	B4	C3	21	9	1
25.ix	16.ix	64	D4	D3	15	9	1
25.ix	21.ix	119	G4	F3	21	4	1
25.ix	21.ix	106	G4	G4	-	4	1
27.ix	15.ix	239	A7	A6	15	*	1
27.ix	25.ix	1/242	C3	B2	21	*	1
27.ix	25.ix	381	B4	B4	-	*	1
27.ix	25.ix	523	C3	D4	21	*	1
27.ix	15.ix	69	E4	E3	15	*	1
27.ix	24.ix	522	E4	F3	21	*	3
27.ix	25.ix	615	G9	F9	15	*	0
28.ix	25.ix	119	F3	E3	15	3	2
29.ix	28.ix	119	E3	E2	15	1	3
29.ix	28.ix	41	E4	E4	-	1	1
29.ix	14.ix	401	D4	F4	30	15	1
30.ix	29.ix	481	E2	E2	-	1	1
30.ix	29.ix	41	E3	E3	-	1	2
30.ix	29.ix	198	E4	F3	21	1	0
1.x	24.ix	413	A7	A6	15	7	1
1.x	30.ix	458	A4	B2	33	1	1
1.x	15.ix	505	G5	F3	33	16	0
4.x	28.ix	650	C6	C6	-	*	1
4.x	30.ix	39	B8	C6	33	*	1
4.x	28.ix	385	A9	C6	53	*	1
4.x	24.ix	336	A7	C7	30	*	1
4.x	24.ix	212	E4	D3	21	*	3
4.x	1.x	233	D6	F7	33	*	1
4.x	14.ix	96	E4	G4	30	*	1
6.x	5.x	187	A7	A7	-	1	2
6.x	25.ix	264	F7	B9	67	11	0
6.x	30.ix	41	E3	E4	15	6	3
6.x	25.ix	601	E7	F6	21	11	1
7.x	21.ix	228	F6	C6	45	16	1
8.x	21.ix	278	F7	E6	21	17	1
8.x	30.ix	198	F3	F4	15	8	2
11.x	8.x	647	B7	A3	62	*	1
11.x	14.ix	320	A7	B10	48	*	1
11.x	24.ix	590	B4	C4	15	*	1
11.x	24.ix	249	E6	D4	33	*	2
12.x	25.ix	64	D3	D4	15	17	0
12.x	22.ix	634	A7	B7	15	22	1
14.x	13.x	590	C4	C4	-	1	3
14.x	8.x	278	E6	D8	33	6	2
18.x	1.x	81	F3	C6	64	*	1
25.x	22.x	107	C2	C2	-	*	2
25.x	14.x	590	C4	D3	21	*	4
25.x	8.x	198	F4	D4	30	*	3
26.x	25.x	590	D3	C4	21	1	5
26.x	27.ix	521	E2	D4	33	29	1
1.xi	8.x	436	B10	E6	75	*	6
2.xi	15.x	340	C7	C6	15	18	2
3.xi	19.x	443	B6	F7	62	15	2
8.ix	21.x	173	C5	A1	67	*	3
19.xi	3.xi	443	F7	G4	48	16	3

Appendix 5.1 (ii): Recapture records for *Nebria brevicollis* adults,
excluding those known to have overwintered 1975-76

(Abbreviations as for App. 5.1(i)).

DRC	DRL	IM	SRL	SRC	d	t	PRC
26.v	25.v	660	D7	C5	33	1	0
26.v	25.v	659	D6	D6	-	1	0
17.ix	14.ix	720	D4	D4	-	3	0
17.ix	15.ix	766	F3	F3	-	2	0
17.ix	16.ix	791	F8	F8	-	1	0
17.ix	16.ix	789	F8	F8	-	1	0
20.ix	17.ix	796	A5	A5	-	*	0
20.ix	14.ix	717	C4	B1	48	*	0
20.ix	15.ix	751	B4	B4	-	*	0
20.ix	16.ix	776	C3	C3	-	*	0
20.ix	14.ix	713	B4	C3	21	*	0
20.ix	14.ix	715	C3	C3	-	*	0
21.ix	14.ix	711	A5	A5	-	7	0
21.ix	14.ix	724	D10	A10	45	7	0
21.ix	17.ix	800	C2	B4	33	4	0
21.ix	14.ix	728	E4	E5	15	7	0
21.ix	17.ix	766	F3	F3	-	4	1
22.ix	21.ix	913	C4	C4	-	1	0
22.ix	21.ix	874	D4	D4	-	1	1
22.ix	21.ix	918	D6	D6	-	1	0
23.ix	21.ix	909	A7	A7	-	2	0
24.ix	16.ix	774	A5	A5	-	8	0
24.ix	22.ix	950	A7	A7	-	2	0
24.ix	23.ix	909	A7	A7	-	1	0
24.ix	23.ix	961	A4	B4	15	1	0
24.ix	23.ix	971	C3	C3	-	1	0
24.ix	14.ix	735	F4	D3	33	10	0
24.ix	14.ix	714	C3	D4	21	10	0
24.ix	23.ix	976	D6	D6	-	1	1
24.ix	23.ix	977	D7	D7	-	1	0
24.ix	21.ix	925	F1	E1	15	3	0
24.ix	15.ix	760	E4	E4	-	9	0
24.ix	17.ix	808	F4	F4	-	7	0
24.ix	15.ix	759	D4	F4	30	9	0
24.ix	14.ix	721	D4	F5	33	10	0
25.ix	23.ix	960	A4	A4	-	2	0
25.ix	24.ix	1002	B4	B4	-	1	0
25.ix	24.ix	1023	D4	D4	-	1	0
25.ix	22.ix	881	D4	D4	-	3	1
25.ix	24.ix	1051	E8	D10	33	1	0
25.ix	24.ix	1047	E4	E3	15	1	0
25.ix	24.ix	1048	E4	E4	-	1	0
25.ix	24.ix	1039	E4	E4	-	1	0
25.ix	22.ix	874	D4	E4	15	3	2
25.ix	17.ix	810	F4	E5	21	8	0
25.ix	24.ix	1051	E5	E5	-	1	0
25.ix	24.ix	1054	E6	E6	-	1	0
25.ix	24.ix	1004	B8	E7	48	1	0

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
25.ix	23.ix	981	E8	E8	-	2	0
25.ix	24.ix	1056	E7	E9	30	1	0
25.ix	14.ix	718	C4	E10	95	11	0
25.ix	21.ix	921	E4	F2	33	4	0
25.ix	17.ix	811	F4	F4	-	8	0
25.ix	21.ix	942	G7	F6	21	4	0
25.ix	17.ix	826	G5	F8	48	8	0
25.ix	17.ix	791	F8	F8	-	8	1
25.ix	23.ix	980	E7	G8	33	2	0
25.ix	24.ix	1062	F9	G9	15	1	0
27.ix	25.ix	865	B4	A3	21	*	1
27.ix	24.ix	1025	D6	A4	53	*	0
27.ix	24.ix	990	A5	A5	-	*	0
27.ix	15.ix	750	A7	A7	-	*	0
27.ix	23.ix	964	A7	A7	-	*	0
27.ix	23.ix	963	A7	A7	-	*	0
27.ix	24.ix	1013	C4	B4	15	*	0
27.ix	21.ix	832	A4	B4	15	*	0
27.ix	17.ix	801	C4	B4	15	*	0
27.ix	17.ix	818	F8	B7	62	*	0
27.ix	21.ix	910	B6	B7	15	*	0
27.ix	15.ix	753	B6	B7	15	*	0
27.ix	25.ix	886	B8	B8	-	*	1
27.ix	21.ix	912	C3	C2	15	*	0
27.ix	22.ix	913	C4	C4	-	*	1
27.ix	21.ix	916	C7	C6	15	*	0
27.ix	24.ix	1016	C7	C8	15	*	0
27.ix	24.ix	1058	E8	C8	30	*	0
27.ix	24.ix	992	A6	C9	53	*	0
27.ix	24.ix	715	C2	D4	33	*	2
27.ix	24.ix	1009	C3	D4	21	*	0
27.ix	22.ix	956	E4	D4	15	*	0
27.ix	17.ix	795	A4	D4	45	*	0
27.ix	25.ix	1023	D4	D4	-	*	1
27.ix	24.ix	888	D10	D8	30	*	0
27.ix	17.ix	819	F8	D10	42	*	0
27.ix	16.ix	788	F4	E2	33	*	0
27.ix	24.ix	1024	D4	E3	21	*	0
27.ix	15.ix	758	D4	E4	15	*	0
27.ix	24.ix	1040	E4	E4	-	*	0
27.ix	14.ix	729	E4	E4	-	*	0
27.ix	17.ix	815	F7	E8	21	*	0
27.ix	14.ix	726	D10	E9	21	*	0
27.ix	25.ix	718	E10	E10	-	*	1
27.ix	25.ix	921	F2	F2	-	*	1
27.ix	14.ix	745	G4	F4	15	*	0
27.ix	25.ix	876	D4	F4	30	*	1
27.ix	24.ix	1022	D4	F4	30	*	0
27.ix	24.ix	808	F4	F5	15	*	0
28.ix	22.ix	954	C6	C3	45	6	0
28.ix	14.ix	742	G4	E2	42	14	0

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
28.ix	24.ix	1011	C3	E3	30	4	0
28.ix	16.ix	770	A4	G2	95	12	0
28.ix	21.ix	914	C6	G4	67	7	0
28.ix	24.ix	721	F5	G5	15	4	1
28.ix	21.ix	936	G4	G7	45	7	0
29.ix	24.ix	998	A7	A5	30	5	0
29.ix	28.ix	1096	B6	A5	21	1	0
29.ix	28.ix	1111	C3	A6	53	1	0
29.ix	24.ix	1001	A7	A7	-	5	0
29.ix	28.ix	1091	B4	B4	-	1	0
29.ix	28.ix	1092	B4	B4	-	1	0
29.ix	28.ix	1095	B6	B6	-	1	0
29.ix	21.ix	872	C7	B6	21	8	1
29.ix	28.ix	1101	B7	B7	-	1	0
29.ix	28.ix	1107	B10	B9	15	1	0
29.ix	28.ix	1112	C6	C2	60	1	0
29.ix	28.ix	954	C3	C3	-	1	1
29.ix	24.ix	1017	C7	C7	-	5	0
29.ix	21.ix	934	F9	C7	53	8	0
29.ix	24.ix	1026	D7	C7	15	5	0
29.ix	28.ix	1116	C10	C10	-	1	0
29.ix	24.ix	989	A4	D10	101	5	0
29.ix	28.ix	1011	E3	E1	30	1	0
29.ix	15.ix	761	E4	E2	30	14	0
29.ix	28.ix	1132	E3	E3	-	1	0
29.ix	28.ix	1133	E3	E3	-	1	0
29.ix	23.ix	970	C3	E4	33	6	0
29.ix	14.ix	739	F7	F3	60	15	0
29.ix	24.ix	1038	E4	F3	21	5	0
29.ix	28.ix	1149	G4	G4	-	1	0
30.ix	29.ix	1096	A5	B6	21	1	1
30.ix	23.ix	972	C3	B7	62	7	0
30.ix	28.ix	1093	B6	C2	62	2	0
30.ix	29.ix	954	C3	C3	-	1	2
30.ix	16.ix	771	A5	C4	33	14	0
30.ix	29.ix	1191	C7	C7	-	1	0
30.ix	25.ix	882	D4	D4	-	5	1
30.ix	28.ix	1120	D4	D4	-	2	0
30.ix	28.ix	1152	G4	D4	45	2	0
30.ix	16.ix	779	D4	E2	33	14	0
1.x	30.ix	954	C3	A3	30	1	3
1.x	29.ix	934	C7	A6	33	2	0
1.x	30.ix	1247	A7	A7	-	1	0
1.x	29.ix	1186	C6	A7	33	2	0
1.x	30.ix	1258	A7	A7	-	1	0
1.x	29.ix	872	B6	A10	62	2	2
1.x	29.ix	1219	E7	B7	45	2	0
1.x	30.ix	1253	B8	B8	-	1	0
1.x	27.ix	963	A7	C7	30	4	1
1.x	30.ix	1255	B9	C7	33	1	0
1.x	28.ix	1148	F10	C7	64	3	0
1.x	30.ix	1260	C10	C10	-	1	0

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
1.x	29.ix	1199	D10	C10	15	2	0
1.x	30.ix	1120	D4	D4	-	1	1
1.x	29.ix	1174	A7	D7	45	2	0
1.x	28.ix	1156	G7	D10	64	3	0
1.x	30.ix	1268	D10	D10	-	1	0
1.x	28.ix	1128	E1	E1	-	3	0
1.x	30.ix	1152	D4	E1	48	1	0
1.x	28.ix	1131	E1	E1	-	3	0
1.x	30.ix	1272	E3	E3	-	1	0
1.x	28.ix	1119	D4	E4	15	3	0
1.x	29.ix	1133	E3	E4	15	2	1
1.x	29.ix	896	G4	E4	30	2	1
1.x	30.ix	1259	C4	E4	30	1	0
1.x	30.ix	1264	D4	E4	15	1	0
1.x	24.ix	899	G9	E10	33	7	1
1.x	30.ix	1280	F3	F3	-	1	0
1.x	25.ix	853	A7	F3	96	6	0
1.x	29.ix	1223	F3	F3	-	2	0
1.x	24.ix	1037	E4	F4	15	7	0
1.x	14.ix	731	E5	F4	21	17	0
1.x	29.ix	1227	F7	F7	-	2	0
1.x	30.ix	1274	E4	F7	48	1	0
1.x	28.ix	1146	F10	F8	30	3	0
1.x	17.ix	821	F8	G7	21	14	0
4.x	1.x	1285	A1	A1	-	*	0
4.x	30.ix	1256	C3	A3	30	*	0
4.x	1.x	1295	A7	A5	30	*	0
4.x	30.ix	1246	A7	A7	-	*	0
4.x	1.x	1258	A7	A7	-	*	0
4.x	17.ix	798	A7	A7	-	*	0
4.x	28.ix	1115	C7	A7	30	*	0
4.x	29.ix	1168	A5	A7	30	*	0
4.x	30.ix	1249	A7	A7	-	*	0
4.x	1.x	1300	A7	B6	21	*	0
4.x	24.ix	1028	D7	B6	33	*	0
4.x	28.ix	1104	B9	B8	15	*	0
4.x	1.x	1146	F8	B8	60	*	0
4.x	1.x	1306	B5	C3	33	*	0
4.x	29.ix	1166	A5	C4	33	*	0
4.x	24.ix	1010	C3	C6	45	*	0
4.x	1.x	1255	C7	C8	15	*	1
4.x	30.ix	1094	B6	D3	53	*	1
4.x	1.x	1307	B5	D4	33	*	0
4.x	24.ix	1052	E5	D4	21	*	0
4.x	1.x	1314	C3	D4	21	*	0
4.x	24.ix	1033	E1	D4	48	*	0
4.x	30.ix	882	D4	D4	-	*	2
4.x	24.ix	759	F4	D4	30	*	0
4.x	29.ix	1226	F7	D6	33	*	0
4.x	29.ix	1187	C6	D6	15	*	0
4.x	29.ix	1216	E7	D7	15	*	0
4.x	25.ix	791	F8	D10	42	*	2

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
4.x	25.ix	826	F8	D10	42	*	0
4.x	1.x	1128	E1	E1	-	*	1
4.x	1.x	1272	E3	E1	30	*	1
4.x	29.ix	1197	D4	E2	33	*	0
4.x	1.x	1264	E4	E3	15	*	1
4.x	24.ix	760	E4	E4	-	*	0
4.x	29.ix	1192	C8	E6	42	*	0
4.x	28.ix	1136	E7	E7	-	*	0
4.x	17.ix	813	F6	E7	21	*	0
4.x	29.ix	1026	C7	E9	42	*	1
4.x	16.ix	787	F4	F3	15	*	0
4.x	29.ix	1222	F3	F4	15	*	0
4.x	1.x	745	F4	F4	-	*	2
4.x	29.ix	1214	E7	F7	15	*	0
4.x	30.ix	1276	E6	F7	21	*	0
4.x	1.x	899	E10	F9	21	*	2
4.x	1.x	1223	F3	G4	21	*	1
4.x	29.ix	1209	E4	G4	30	*	0
4.x	22.ix	958	F4	G5	21	*	0
4.x	29.ix	1181	B9	G7	80	*	0
4.x	28.ix	1143	F4	G7	48	*	0
4.x	28.ix	1078	A7	G7	90	*	0
4.x	17.ix	807	E8	G8	30	*	0
5.x	29.ix	1224	F6	B6	60	6	0
5.x	1.x	1309	B8	B8	-	4	0
5.x	25.ix	1048	E4	E4	-	10	1
5.x	16.ix	783	E5	E7	30	19	0
6.x	21.ix	924	E4	A5	62	15	0
6.x	1.x	1244	D1	A7	101	5	0
6.x	22.ix	951	B4	A7	48	14	0
6.x	24.ix	997	A7	B7	15	12	0
6.x	1.x	1310	B8	B9	15	5	0
6.x	1.x	1297	A7	C6	33	5	0
6.x	28.ix	1135	E7	C7	30	8	0
6.x	28.ix	1114	C6	C7	15	8	0
6.x	5.x	1475	C7	C7	-	1	0
6.x	1.x	888	C6	D6	15	5	3
6.x	24.ix	1053	E6	D6	15	12	0
6.x	28.ix	1075	A5	E2	75	8	0
6.x	24.ix	714	D4	E4	15	12	0
6.x	1.x	1120	D4	E4	15	5	2
6.x	14.ix	743	G4	E4	30	22	0
6.x	28.ix	1158	G7	E6	33	8	0
6.x	28.ix	1428	E9	E9	-	8	0
6.x	28.ix	1155	G7	E9	42	8	0
6.x	28.ix	1138	E9	E10	15	8	0
6.x	24.ix	1060	F3	F4	15	12	0
6.x	30.ix	1269	E1	F4	48	6	0
6.x	25.ix	1054	E6	F6	15	11	0
6.x	5.x	1478	F6	F6	-	1	0
6.x	28.ix	1153	G8	F7	21	8	0
6.x	28.ix	1125	D8	F8	30	8	0

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
6.x	5.x	1479	G4	G4	-	1	0
7.x	21.ix	911	B7	A7	15	16	0
7.x	29.ix	1175	A7	B8	21	8	0
7.x	1.x	1313	C2	B8	91	6	0
7.x	1.x	1156	D10	B10	30	6	0
7.x	24.ix	1041	E4	D4	15	13	0
7.x	29.ix	1211	E4	D4	15	8	0
7.x	14.ix	747	G8	E2	95	23	0
7.x	24.ix	1019	D4	E4	15	13	0
7.x	28.ix	1123	D4	E4	15	9	0
8.x	7.x	1572	G9	A9	90	1	0
8.x	1.x	647	A9	B7	33	7	1
8.x	7.x	1423	C7	C7	-	1	1
8.x	7.x	1094	D3	D3	-	1	3
8.x	7.x	1041	D4	D4	-	1	1
8.x	28.ix	1142	F3	D4	33	10	0
8.x	5.x	1394	D7	D7	-	3	0
8.x	1.x	1253	B8	A7	21	7	0
8.x	7.x	1557	E9	E9	-	1	0
8.x	7.x	1549	D4	F2	42	1	0
8.x	7.x	1558	F3	F3	-	1	0
11.x	7.x	1175	B8	A7	21	*	0
11.x	8.x	1576	A7	A7	-	*	0
11.x	15.ix	755	C4	A7	53	*	0
11.x	7.x	1491	B9	A7	33	*	0
11.x	24.ix	774	A5	A7	30	*	1
11.x	30.ix	1278	E9	B6	64	*	0
11.x	8.x	1166	B8	B8	-	*	2
11.x	1.x	1303	A10	B9	21	*	0
11.x	1.x	963	C7	B10	48	*	2
11.x	24.ix	909	A7	B10	48	*	0
11.x	24.ix	1047	E4	C4	30	*	0
11.x	8.x	1423	C7	C6	15	*	2
11.x	21.ix	728	E5	C6	33	*	1
11.x	29.ix	1189	C7	C6	15	*	0
11.x	30.ix	1250	A7	C6	33	*	0
11.x	23.ix	962	A6	D2	75	*	0
11.x	1.x	1247	A7	D4	64	*	0
11.x	8.x	1581	D4	D4	-	*	0
11.x	15.ix	756	C5	D4	21	*	0
11.x	7.x	1410	G4	D4	45	*	1
11.x	8.x	1585	E1	D4	48	*	0
11.x	7.x	1571	G9	D6	64	*	0
11.x	8.x	1394	D7	D6	15	*	1
11.x	8.x	1494	G4	D10	101	*	0
11.x	8.x	1583	D10	D10	-	*	0
11.x	7.x	1553	E4	E1	45	*	0
11.x	29.ix	1194	D1	E1	15	*	0
11.x	7.x	1211	D4	E2	33	*	1
11.x	8.x	1579	D3	E2	21	*	0
11.x	21.ix	907	A7	E3	85	*	0
11.x	25.ix	1039	E4	E3	15	*	1

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
11.x	8.x	1580	D4	E4	15	*	0
11.x	7.x	1561	F6	E5	21	*	0
11.x	28.ix	1080	A7	E6	62	*	0
11.x	8.x	1524	F6	E6	15	*	1
11.x	5.x	1309	B8	E6	53	*	1
11.x	21.ix	923	E4	E6	30	*	0
11.x	8.x	1599	G10	E10	30	*	0
11.x	8.x	1549	F2	F2	-	*	1
11.x	8.x	1520	F3	F3	-	*	1
11.x	8.x	1041	D4	F3	33	*	2
11.x	29.ix	1207	E3	F4	21	*	0
11.x	8.x	1040	F3	F4	15	*	2
11.x	1.x	750	C6	F6	45	*	2
11.x	5.x	1477	E7	F7	15	*	0
11.x	8.x	1594	F8	F8	-	*	0
11.x	7.x	1560	F3	F8	75	*	0
11.x	22.ix	952	C3	F8	87	*	0
11.x	7.x	1567	G5	G4	15	*	0
11.x	8.x	819	G9	G9	-	*	2
12.x	5.x	1423	A7	A7	-	7	0
12.x	29.ix	1213	E6	B4	53	13	0
12.x	7.x	1339	B6	B6	-	5	0
12.x	1.x	1268	D10	B9	33	11	0
12.x	1.x	1260	C10	C6	60	11	0
12.x	30.ix	1245	A5	E7	67	12	0
12.x	7.x	1556	E9	E7	30	5	0
12.x	28.ix	1134	E7	E7	-	14	0
12.x	7.x	1570	G8	E9	33	5	0
12.x	1.x	1280	F3	F2	15	11	0
12.x	24.ix	991	A6	F4	80	18	0
12.x	8.x	1592	F6	G6	15	4	0
13.x	23.ix	979	E7	B6	48	20	0
13.x	5.x	1048	E4	C6	42	8	2
13.x	1.x	1133	E4	E3	15	12	2
13.x	24.ix	1029	D7	E7	15	19	0
13.x	8.x	1536	E6	F4	33	5	0
13.x	5.x	1435	F4	G2	33	8	0
13.x	8.x	1094	D3	G2	48	5	3
14.x	13.x	1611	B4	B4	-	1	1
14.x	13.x	1745	A5	C4	33	1	0
14.x	13.x	1048	C6	C6	-	1	3
14.x	1.x	1199	C10	C8	30	13	1
14.x	8.x	1587	E6	E1	75	6	0
14.x	7.x	1573	G9	E6	53	7	0
14.x	13.x	1756	E9	E9	-	1	0
14.x	28.ix	1098	B7	F6	62	16	0
14.x	5.x	1476	D10	G9	48	9	0
15.x	28.ix	1013	D3	A1	53	17	0
15.x	29.ix	11/1205	E2	A7	96	16	0
15.x	7.x	1544	C7	A7	30	8	0
15.x	14.x	1765	B7	B7	-	1	0
15.x	7.x	1546	C9	B10	21	8	0
15.x	14.x	798	C6	C6	-	1	2

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
15.x	13.x	774	A7	C8	33	2	3
15.x	14.x	1199	C8	C8	-	1	2
15.x	24.ix	1014	C6	D4	33	21	0
15.x	8.x	1598	G8	D4	75	7	0
15.x	13.x	1748	D3	D4	15	2	0
15.x	21.ix	927	F6	D6	30	24	0
15.x	13.x	1761	G9	D10	48	2	0
15.x	17.ix	806	E5	E2	45	28	0
15.x	14.x	1650	E5	E5	-	1	1
15.x	8.x	1479	G4	F4	15	7	2
15.x	13.x	907	E3	F4	21	2	3
15.x	29.ix	1242	G9	F8	21	16	0
15.x	13.x	1040	E4	G4	30	2	5
15.x	5.x	783	E7	G4	53	10	1
15.x	7.x	1554	E4	G4	30	8	0
15.x	13.x	1029	E7	G7	30	2	1
18.x	14.x	1770	E2	A5	75	*	0
18.x	15.x	1786	A7	A7	-	*	0
18.x	29.ix	1220	E9	B6	64	*	0
18.x	5.x	990	B6	B6	-	*	2
18.x	8.x	1578	C7	B7	15	*	0
18.x	15.x	1546	B10	B9	15	*	1
18.x	15.x	1378	C4	C4	-	*	1
18.x	14.x	1767	C6	C4	30	*	0
18.x	15.x	1321	C6	C6	-	*	1
18.x	29.ix	868	D4	C6	33	*	1
18.x	15.x	1791	C6	C6	-	*	0
18.x	13.x	1747	C6	C9	45	*	0
18.x	15.x	1598	D4	D3	15	*	1
18.x	14.x	1723	E4	D4	15	*	1
18.x	14.x	1573	E6	D4	33	*	1
18.x	15.x	1789	C3	E4	33	*	0
18.x	14.x	813	E7	E6	15	*	3
18.x	14.x	1768	C7	F4	64	*	0
18.x	29.ix	1239	G7	F6	21	*	0
18.x	8.x	1593	F6	F7	15	*	0
18.x	15.x	1811	G5	G4	15	*	0
18.x	15.x	1554	G4	G4	-	*	1
18.x	14.x	1594	G9	G9	-	*	2
19.x	15.x	1473	A7	A7	-	4	2
19.x	13.x	1576	A7	A7	-	6	2
19.x	29.ix	1165	A4	A7	45	20	0
19.x	13.x	1608	A7	A9	30	6	1
19.x	18.x	1823	A7	B4	48	1	0
19.x	28.ix	1082	A7	B7	15	21	0
19.x	18.x	1546	B9	B9	-	1	2
19.x	13.x	1047	C4	C3	15	6	2
19.x	18.x	1598	D3	D3	-	1	2
19.x	18.x	1830	D3	D3	-	1	0
19.x	25.ix	942	F6	D6	30	24	0
19.x	28.ix	721	G5	E2	53	21	2
19.x	18.x	1414	E3	E3	-	1	1
19.x	18.x	1833	E3	E3	-	1	0

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
19.x	7.x	747	E2	E3	15	12	1
19.x	18.x	1638	E3	E3	-	1	1
19.x	15.x	1648	D4	E4	15	4	1
19.x	28.ix	1154	G6	E6	30	21	0
19.x	20.ix	898	F3	F3	-	29	0
19.x	8.x	1586	E4	F4	15	11	0
19.x	14.x	1668	F4	G4	15	5	1
19.x	15.x	1814	G6	G5	15	4	0
20.x	14.x	1769	C7	D6	21	6	0
20.x	15.x	1790	C3	E4	33	5	0
20.x	15.x	1799	E7	E6	15	5	0
20.x	30.ix	1279	F3	G4	21	20	0
21.x	29.ix	1190	C7	A7	30	22	0
21.x	20.x	1875	B8	B8	-	1	0
21.x	18.x	1378	C4	C4	-	3	2
21.x	15.x	1809	F8	C6	53	6	0
21.x	20.x	1790	E4	E2	30	1	1
21.x	14.x	1280	F2	E4	33	7	3
21.x	15.x	1748	D4	G4	45	6	1
21.x	14.x	1766	B7	G9	80	7	0
22.x	21.x	1190	A7	A7	-	1	1
22.x	21.x	1875	B8	B8	-	1	1
22.x	21.x	1809	C6	C6	-	1	1
22.x	29.ix	1221	E9	E9	-	23	0
22.x	13.x	1754	E7	F4	48	9	0
22.x	21.x	1668	G4	G4	-	1	3
22.x	24.ix	1057	E7	G5	42	28	0
25.x	22.x	1659	B7	A5	33	*	1
25.x	14.x	1048	C6	A5	33	*	4
25.x	22.x	1322	A7	A7	-	*	1
25.x	15.x	1544	A7	A8	15	*	1
25.x	25.ix	980	G8	B6	80	*	1
25.x	8.x	1323	C4	C2	30	*	1
25.x	18.x	1220	B6	C2	62	*	1
25.x	18.x	1767	C4	C4	-	*	1
25.x	19.x	1644	E4	D4	15	*	1
25.x	22.x	1897	E1	E1	-	*	0
25.x	13.x	1536	F4	E2	33	*	2
25.x	15.x	1804	F4	E4	15	*	0
25.x	22.x	1221	E9	E9	-	*	1
25.x	29.ix	1235	F10	F3	105	*	1
25.x	15.x	1761	D10	F6	67	*	1
25.x	22.x	1516	F7	F7	-	*	1
25.x	15.x	1029	G7	F8	21	*	2
25.x	13.x	1749	D6	F9	53	*	0
25.x	22.x	1223	G2	G2	-	*	4
25.x	22.x	1900	G4	G4	-	*	0
25.x	22.x	1359	G4	G4	-	*	2
25.x	22.x	1901	G5	G5	-	*	0
25.x	15.x	1807	F7	G7	15	*	0
26.x	25.x	1544	A8	A8	-	1	2

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
26.x	25.x	1903	B6	B6	-	1	0
26.x	25.x	980	B6	B6	-	1	2
26.x	1.x	1294	A7	B7	15	25	0
26.x	25.x	1607	B9	B9	-	1	1
26.x	13.x	1379	C4	C4	-	13	2
26.x	22.x	1010	C4	C4	-	4	3
26.x	25.x	1767	C4	C4	-	1	2
26.x	14.x	1375	E7	C6	33	12	1
26.x	25.x	781	D4	D3	15	1	1
26.x	18.x	1840	F3	D4	33	8	0
26.x	8.x	1466	E4	D4	15	18	1
26.x	8.x	1458	F3	D4	33	18	1
26.x	25.x	1910	D7	D7	-	1	0
26.x	13.x	1571	D6	E6	15	13	2
26.x	7.x	1545	C8	E7	33	19	0
26.x	25.x	1235	F3	F3	-	1	1
26.x	25.x	1646	F3	F3	-	1	1
26.x	25.x	1761	F6	F7	15	1	2
26.x	25.x	1918	F9	F9	-	1	0
26.x	14.x	1720	D6	G6	45	12	1
27.x	14.x	1756	E9	B7	53	13	1
27.x	20.x	1881	G4	F4	15	7	0
27.x	14.x	1773	F7	F8	15	13	0
28.x	13.x	1556	E7	B7	45	15	0
28.x	18.x	1143	B6	B7	15	10	2
28.x	28.ix	1110	C3	C4	15	30	0
28.x	18.x	1135	C6	C6	-	10	2
28.x	27.x	1940	E1	E1	-	1	0
28.x	13.x	1752	E1	E1	-	15	0
29.x	15.x	1800	E7	B6	48	14	0
29.x	13.x	1751	D6	B7	33	16	0
29.x	1.x	1305	B4	B7	45	28	0
29.x	14.x	1664	C4	C6	30	15	1
29.x	28.x	1423	C7	C7	-	1	5
29.x	27.x	1526	D10	D10	-	2	2
29.x	28.x	1950	E3	E3	-	1	0
29.x	21.x	1246	E6	E3	45	8	3
1.xi	29.x	980	B6	B6	-	*	4
1.xi	28.x	1467	C4	C4	-	*	3
1.xi	29.x	1963	C5	C5	-	*	0
1.xi	29.x	1965	E1	E1	-	*	0
1.xi	28.x	1946	C4	E4	30	*	0
1.xi	7.x	1568	G6	F4	33	*	0
1.xi	21.x	1693	C7	F8	48	*	2
1.xi	13.x	1435	G2	G2	-	*	1
1.xi	28.x	1957	G5	G4	15	*	0
1.xi	14.x	1778	G5	G5	-	*	0
2.xi	20.x	1360	A4	C4	30	13	2
2.xi	27.x	1010	C4	C4	-	6	4
2.xi	29.x	1664	C6	C6	-	4	2
2.xi	21.x	861	A7	E7	60	13	1
2.xi	15.x	1413	E2	F4	33	18	2

Appendix 5.1 (ii): (Continued)

DRC	DRL	IM	SRL	SRC	d	t	PRC
3.xi	2.xi	1010	C4	C4	-	1	5
3.xi	2.xi	1134	C4	C4	-	1	2
3.xi	20.x	1396	F7	G7	15	14	2
5.xi	27.x	1691	A7	A7	-	9	1
5.xi	4.xi	1993	B1	B1	-	1	0
5.xi	15.x	1610	A7	C4	53	21	1
5.xi	29.x	1869	E4	E4	-	7	1
5.xi	14.x	1456	G6	E4	42	22	3
5.xi	8.x	1369	G7	E6	33	28	1
8.xi	28.x	1556	B7	A7	15	*	2
8.xi	15.x	1798	E7	A7	60	*	0
8.xi	5.xi	1239	B9	B9	-	*	2
8.xi	22.x	1717	E4	D4	15	*	1
8.xi	28.x	1951	E4	E1	45	*	0
8.xi	27.x	1671	G4	E2	42	*	1
8.xi	15.x	1794	D6	E6	15	*	0
8.xi	13.x	1750	D6	E6	15	*	0
8.xi	29.x	1967	E7	E7	-	*	0
8.xi	13.x	1759	F4	F3	15	*	0
8.xi	15.x	1805	F4	F3	15	*	0
8.xi	2.xi	1990	G6	G6	-	*	0
8.xi	14.x	1779	G6	G7	15	*	0
11.xi	2.xi	1413	F4	A1	87	*	3
12.xi	27.x	1485	C6	E7	33	16	1
12.xi	11.xi	100/205	G5	G5	-	1	1
15.xi	12.xi	1778	G5	G5	-	*	2
16.xi	21.x	1723	D4	F4	30	26	3
17.xi	2.xi	755	B6	A7	21	15	4
17.xi	8.xi	1951	E1	E1	-	9	0
18.xi	3.xi	1010	C4	C4	-	15	6
18.xi	2.xi	1360	C4	C4	-	16	3
19.xi	29.x	1800	B6	C6	15	21	1
19.xi	2.xi	1946	F3	G6	48	17	2
22.xi	17.xi	1524	C6	C7	15	*	5
22.xi	17.xi	1/223	E1	E1	-	*	0
22.xi	18.xi	1/211	E1	E1	-	*	1
22.xi	11.xi	1/212	E7	E7	-	*	3
23.xi	22.xi	1524	C7	C7	-	1	6
24.xi	12.xi	1485	E7	E6	15	12	2
29.xi	19.xi	1946	G6	E6	30	*	3
29.xi	24.xi	1485	E6	E7	15	*	3
29.xi	26.xi	1560	G4	G4	-	*	3
8.xii	7.xii	1433	E1	E1	-	1	1
21.i	6.i	1/254	C5	E8	53	15	0
18.ii	17.ii	1921	E4	E4	-	1	1
4.iii	8.ii	1298	A7	A7	-	24	2
7.iii	2.iii	1997	F3	E4	21	*	2

Appendix 5.2 (i): Recapture records for Pterostichus madidus adultsknown to have overwintered 1975-76

(Abbreviations as per Appendix 5.1)

(a) Male Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
25.iii	17.iii	63	A5	A5	-	8	1
25.iii	12.iii	74	B10	B10	-	13	0
25.iii	15.iii	80	G4	G4	-	10	0
26.iii	25.iii	105	B8	B8	-	1	0
31.iii	30.iii	138	B3	B3	-	1	0
1.iv	29.iii	133	F7	F7	-	3	0
12.iv	25.iii	63	A5	A5	-	*	2
12.iv	6.iv	198	E6	E6	-	*	0
14.iv	13.iv	290	A6	A6	-	1	0
14.iv	12.iv	271	G3	G3	-	2	0
6.v	12.iv	256	F1	F1	-	24	0
6.v	14.iv	308	F7	F7	-	22	0
6.v	14.iv	309	G3	G3	-	22	0
7.v	6.v	384	E9	E9	-	1	0
10.v	7.v	449	F6	F6	-	*	0
10.v	6.v	351	A2	A2	-	*	0
17.v	6.v	411	G6	G6	-	*	0
20.v	19.v	591	E2	E2	-	1	0
24.v	6.v	386	F1	F1	-	*	0
1.vi	6.v	369	C8	C8	-	*	0
3.vi	1.vi	726	C9	C9	-	2	0
3.vi	4.v	317	D8	D8	-	30	0
4.vi	3.vi	790	E2	E2	-	1	0
7.vi	3.vi	726	C9	D8	21	*	0
7.vi	1.vi	727	C9	D9	15	*	0
8.vi	7.vi	825	A4	A4	-	1	0
9.vi	1.vi	741	D9	D9	-	8	0
14.vi	27.v	678	C6	A8	42	*	0
14.vi	24.v	622	D3	D6	45	*	0
16.vi	14.vi	1056	F7	F7	-	2	0
17.vi	16.vi	1096	B4	B4	-	1	0
17.vi	10.vi	971	C2	C1	15	7	0
17.vi	16.vi	1/27	G3	G3	-	1	0
18.vi	1.vi	705	A7	F10	87	17	0
21.vi	14.vi	1047	E5	E6	15	*	0
21.vi	24.v	637	F2	F3	15	*	0
24.vi	16.vi	1/30	G8	D6	53	8	0
25.vi	24.vi	L/19	C2	C2	-	1	0
25.vi	23.vi	1/185	F3	F3	-	2	0
25.vi	3.vi	801	G6	G4	30	22	0
28.vi	14.vi	1035	E3	E3	-	*	0
28.vi	24.vi	L/33	E5	E3	30	*	0
28.vi	24.vi	L/35	F10	F10	-	*	0
29.vi	16.vi	1/1	C5	B5	15	13	0
29.vi	4.vi	816	F2	G3	21	25	0
2.vii	25.vi	L/47	B2	B2	-	7	0
5.vii	14.vi	1006	A7	D6	48	*	0

Appendix 5.2 (i): (Continued)

(a) Male Beetles (Cont)

DRC	DRL	IM	SRL	SRC	d	t	PRC
5.vii	22.vi	1/154	F3	E3	15	*	0
7.vii	16.vi	1097	B4	A4	15	21	0
8.vii	22.vi	1/141	C8	C7	15	16	0
20.vii	8.vii	1/202	A4	A5	15	12	0
22.vii	22.vi	1/136	B6	B4	30	30	0
27.vii	26.vii	1094	E5	E6	15	1	1
30.viii	25.viii	912	A3	A3	-	*	1
30.viii	2.viii	105	E6	B6	45	*	2

(b) Female Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
17.iii	11.iii	50	C4	C4	-	6	1
17.iii	12.iii	77	F8	F8	-	5	0
18.iii	17.iii	90	C2	C2	-	1	0
25.iii	17.iii	91	C7	C7	-	8	0
26.iii	22.iii	98	B6	B6	-	4	0
26.iii	19.iii	96	G6	G6	-	7	0
29.iii	26.iii	113	D4	D4	-	*	0
1.iv	31.iii	151	B9	B9	-	1	0
1.iv	31.iii	155	F3	F3	-	1	0
2.iv	1.iv	162	C6	C6	-	1	0
9.iv	6.iv	193	C9	C9	-	3	0
9.iv	1.iv	167	F3	F3	-	8	0
9.iv	5.iv	184	G2	G2	-	4	0
12.iv	1.iv	157	A5	A5	-	*	0
12.iv	2.iv	162	C6	C6	-	*	0
12.iv	5.iv	183	D1	D1	-	*	0
13.iv	12.iv	268	G2	G2	-	1	0
13.iv	1.iv	172	G9	F10	21	12	0
14.iv	6.iv	191	C5	C5	-	8	0
14.iv	13.iv	295	F1	F1	-	1	0
14.iv	13.iv	172	F10	F10	-	1	1
14.iv	13.iv	299	G3	G3	-	1	0
6.v	12.iv	231	A2	A2	-	24	0
7.v	6.v	309	G3	G3	-	1	1
10.v	6.v	397	F6	F6	-	*	0
10.v	7.v	433	D10	D10	-	*	0
10.v	6.v	412	G6	G6	-	*	0
10.v	7.v	461	G6	G6	-	*	0
11.v	10.v	499	F6	F6	-	1	0
12.v	10.v	497	F6	F6	-	2	0
12.v	10.v	502	F6	F6	-	2	0
12.v	11.v	529	G6	G6	-	1	0
17.v	12.v	529	G6	G6	-	*	1
18.v	17.v	559	B8	B8	-	1	0
18.v	10.v	461	G6	G6	-	8	0
19.v	18.v	559	B8	B8	-	1	0

Appendix 5.2 (i): (Continued)(b) Female Beetles (cont)

DRC	DRL	IM	SRL	SRC	d	t	PRC
19.v	11.v	517	D1	D1	-	8	0
24.v	21.v	598	F1	F1	-	*	0
24.v	10.v	506	F6	F6	-	*	0
24.v	17.v	571	G2	G2	-	*	0
25.v	24.v	608	B1	B1	-	1	0
26.v	12.v	537	B9	B9	-	14	0
1.vi	24.v	614	C1	C1	-	*	0
1.vi	20.v	594	G2	G2	-	*	0
2.vi	7.v	435	E1	C1	30	26	0
2.vi	24.v	625	E2	E2	-	9	0
15.vi	2.vi	777	G5	G5	-	13	0
24.vi	23.vi	1/194	G6	G6	-	1	0

Appendix 5.2 (ii): Recapture records for Pterostichus madidus adults
excluding those known to have overwintered 1975-76.

(Abbreviations as per Appendix 5.1).

(a) Male Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
22.vii	20.vii	1/220	B10	B10	-	2	0
26.vii	23.vii	1/262	D6	D6	-	*	0
26.vii	23.vii	1/264	D10	D10	-	*	0
27.vii	26.vii	1/316	G2	G2	-	1	0
28.vii	21.vii	1/236	B7	B7	-	7	0
29.vii	28.vii	1/236	B7	B7	-	1	1
29.vii	26.vii	1/280	B10	B10	-	3	0
30.vii	23.vii	1/256	A10	A10	-	7	0
3.viii	2.viii	1/421	D3	D3	-	1	0
4.viii	2.viii	1/425	D7	D7	-	2	0
5.viii	30.vii	1/385	A10	E7	75	6	0
10.viii	9.viii	1/517	G2	G2	-	1	0
11.viii	28.vii	1/367	F2	F2	-	14	0
12.viii	11.viii	1/547	A10	A10	-	1	0
12.viii	5.viii	1/481	F2	G2	15	7	0
16.viii	28.vii	1/359	C7	D6	21	*	0
16.viii	13.viii	1/585	E6	E6	-	*	0
16.viii	2.viii	1/431	G2	G2	-	*	0
16.viii	13.viii	1/590	G9	G9	-	*	0
18.viii	17.viii	1/640	A8	A8	-	1	0
23.viii	4.viii	1/460	D4	D4	-	*	0
23.viii	16.viii	1/616	D10	D10	-	*	0
23.viii	12.viii	1/481	G2	F2	15	*	0
23.viii	4.viii	1/466	F2	F2	-	*	0
25.viii	24.viii	1/726	B4	B4	-	1	0
25.viii	23.viii	1/719	G1	G1	-	2	0
26.viii	25.viii	1/739	E6	E6	-	1	0
30.viii	16.viii	1/601	B4	B4	-	*	0
30.viii	3.viii	1/443	B7	A8	21	*	0
30.viii	20.viii	1/683	B10	B9	15	*	0
30.viii	16.viii	1/610	D3	D4	15	*	0
30.viii	17.viii	1/650	G9	F9	15	*	0
31.viii	6.viii	1/486	B7	D8	33	25	0
31.viii	16.viii	1/606	C8	D6	33	15	0
20.ix	31.viii	1/763	C10	D10	15	*	1
21.x	18.x	1/856	C7	C7	-	3	0
25.x	15.x	1/854	D10	D10	-	*	0
1.xi	12.x	1/844	B7	B7	-	*	0
5.xi	1.xi	1/844	B7	B7	-	4	1

Appendix 5.2 (ii): (Continued)

(b) Female Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
30.vii	27.vii	1/330	B3	B3	-	3	0
24.viii	19.viii	1/670	A7	A7	-	5	0
24.viii	23.viii	1/708	C8	C8	-	1	0
25.viii	16.viii	1/604	B9	B9	-	9	0
11.xi	8.xi	1/909	B6	B6	-	*	0
15.xi	2.xi	1/896	D10	D10	-	*	0
16.xi	15.xi	1/923	D8	D8	-	1	0
17.xi	16.xi	1/925	G4	G4	-	1	0
18.xi	6.xi	1/899	B7	B6	15	12	0
22.xi	19.xi	1/941	E9	E9	-	*	0
26.xi	6.xi	1/901	F5	F5	-	*	0
29.xi	26.xi	1/901	F5	F5	-	*	1
29.xii	29.xi	1/947	C10	C10	-	*	0
24.i	29.xii	1/947	C10	C10	-	*	1
18.iii	14.iii	1/980	E9	E9	-	4	0

Appendix 5.3: Recapture records of Abax parallelepipedus adults

(Abbreviations as per Appendix 5.1)

(a) Male Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
10.v	7.v	52	C3	C3	-	*	0
19.v	10.v	79	F5	F5	-	9	0
24.v	21.v	117	B8	B8	-	*	0
24.v	7.v	60	G4	F4	15	*	0
25.v	24.v	121	B6	B6	-	1	0
26.v	6.v	29	B5	A4	21	20	0
3.vi	10.v	78	F5	F5	-	24	0
4.vi	24.v	123	C9	C9	-	11	0
8.vi	25.v	135	B9	C9	15	14	0
10.vi	18.v	103	D6	E6	15	23	0
11.vi	25.v	140	G10	F10	15	17	0
14.vi	8.vi	212	D6	C9	48	*	0
16.vi	26.v	141	E3	E3	-	21	0
18.vi	17.vi	261	C9	C9	-	1	0
21.vi	1.vi	149	A2	A2	-	*	0
22.vi	21.vi	206	F3	F3	-	1	0
23.vi	18.vi	261	C9	C8	15	5	1
23.vi	16.vi	15	E5	F6	21	7	1
28.vi	4.vi	123	C9	C9	-	*	1
28.vi	2.vi	179	E6	D5	21	*	0
28.vi	2.vi	177	D4	E6	33	*	0
1.vii	21.vi	284	D2	D2	-	10	0
2.vii	18.vi	274	C5	C5	-	14	0
2.vii	29.vi	345	C5	C5	-	3	0
2.vii	21.vi	282	C10	C10	-	11	0
5.vii	24.vi	306	D5	D5	-	*	0
6.vii	10.vi	224	G3	G3	-	26	0
7.vii	17.vi	259	A2	A2	-	20	0
8.vii	1.vii	355	B2	B2	-	7	0
9.vii	2.vii	345	C5	C5	-	7	0
9.vii	14.vi	237	E3	E3	-	25	0
28.vii	27.vii	71	B4	B4	-	1	1
29.vii	28.vii	416	G1	G1	-	1	0
4.viii	28.vii	71	B4	B4	-	7	2
18.viii	20.vii	375	C6	C6	-	29	0
26.viii	24.vii	G	D10	E10	15	2	1
30.viii	2.viii	342	D6	D6	-	*	1
24.ix	20.ix	442	F2	F2	-	4	0

(b) Female Beetles

DRC	DRL	IM	SRL	SRC	d	t	PRC
7.v	6.v	36	D10	D10	-	1	0
10.v	7.v	53	D6	D6	-	*	0
10.v	7.v	57	F6	G7	21	*	0
10.v	6.v	27	A9	B9	15	*	1
9.vi	3.vi	189	E3	E3	-	6	0
15.vi	14.vi	233	C8	C8	-	1	0
24.vi	9.vi	214	A9	A9	-	15	0
1.vii	30.vi	351	A2	A2	-	1	0

Appendix 5.4: Recapture results for other species

Agonum assimile : 5 individuals released marked, 1 only recaptured.

Capture dates 12.5.1977 and 4.4.1978: same trap, 327 days after release.

A. muelleri : 12 individuals released marked : no recaptures

Amara aenea : 9 individuals released marked : no recaptures

Calathus fuscipes: 289 individuals released marked: 2 recaptured.

(i) Capture dates: 29.7.1976 and 5.8.1976 : same trap, 7 days later (♂)

(ii) Capture dates: 13.8.1976 and 30.8.1976: 21m travelled, 17 days (♀)

C. piceus : 232 individuals released marked : 8 recaptured

(i) Capture dates : 6.5.1976 and 14.9.1976 : 48m travelled, 130 days

(ii) Capture dates : 17.5.1976 and 18.5.1976 : same trap, 1 day

(iii) Capture dates : 20.7.1976 and 30.7.1976 : same trap, 10 days (callow)

(iv) Capture dates : 20.7.1976 and 23.8.1976 : 15m travelled, 34 days
(callow)

(v) Capture dates : 9.8.1976 and 11.8.1976 : same trap, 2 days

(vi) Capture dates : 15.9.1976 and 26.6.1977 : 34m travelled, 284
days (♂)

(vii) Capture dates : 18.8.1977 and 25.8.1977 : 34m travelled, 7 days

(viii) Capture dates : 3.5.1977 and 23.6.1977 : 34m travelled, 51 days

Cychrus caraboides : 15 individuals released marked : no recaptures

Leistus ferrugineus: 6 individuals released marked : no recaptures

L. fulvibarbis : 14 individuals released marked : 5 recaptures

(i) Capture dates : 20.9.1977 and 19.10.1977 : 21m travelled, 29 days

(ii) Capture dates : 28.9.1977 and 4.10.1977 : same trap, 6 days

(iii) Capture dates : 13.10.1977 and 25.10.1977 : same trap, 12 days

(iv) Capture dates : 14.10.1977 and 11.11.1977 : same trap, 28 days (♂)

(v) Capture dates : 20.10.1977 and 25.10.1977 : same trap, 6 days (♂)

Appendix 5.4: (Continued)

L. rufomarginatus : 76 individuals released marked : no recaptures

L. spinibarbis : 10 individuals released marked : 2 recaptures

(i) Capture dates : 19.10.1977 and 29.12.1977 : same trap, 71 days

(♀)

(ii) Capture dates : 31.10.1977 and 15.12.1977 : same trap, 45 days

(♀)

Pterostichus nigrita: 17 individuals released marked : no recaptures

Stomis pumicatus : 4 individuals released marked : one recapture

Capture dates : 1.11.1976 and 22.11.1976 : same trap, 21 days

Appendix 6.1: (Continued)

Date	Release Distance	Beetles released:												
		<u>N. brevicollis</u>		<u>P. madidus</u>		<u>Abax parallelepipedus</u>		<u>P. niger</u>		<u>C. violaceus</u>				
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀			
June 17	2m	-	-	4	-	1	-	-	-	-	-	-	-	-
20*	1	-	-	3	4	1	1	-	-	-	-	-	-	-
21	1	-	-	-	2	-	-	-	-	-	-	-	-	-
22	2	-	-	2	5	-	-	-	-	-	-	-	-	-
23	2	-	-	14	8	-	-	-	-	-	-	-	-	-
24	15	-	-	6	6	3	2	-	-	-	-	-	-	-
26*	1	1	1	13	4	2	2	-	-	-	-	-	-	-
29*	1	no further captures until end of August		25	10	8	1	-	-	-	-	-	-	-
30	2	-	-	13	5	5	3	-	-	-	-	-	-	-
July 1	1	-	-	13	4	1	-	-	-	-	-	-	-	-
19	1	-	-	9	1	-	-	-	-	-	-	-	-	-
20	1	-	-	5	1	-	-	-	-	-	-	-	-	-
21	15	-	-	3	1	1	-	-	-	-	-	-	-	-
22	15	-	-	1	1	-	-	-	-	-	-	-	-	-
25*	15	-	-	21	6	6	1	-	-	-	-	-	-	-
26	4	-	-	-	2	3	1	-	-	-	-	-	-	-
27	4	-	-	1	1	4	1	-	-	-	-	-	-	-
28	4	-	-	1	1	2	1	-	-	-	-	-	-	-
29	4	-	-	1	1	1	1	-	-	-	-	-	-	-
Aug 1 *	4	-	-	8	3	-	-	-	-	-	-	-	-	-
2	8	-	-	10	2	2	5	-	-	-	-	-	-	-
6(7)*	1	-	-	16	1	10	5	-	-	-	-	-	-	-
7(8)*	1	-	-	7	-	3	1	-	-	-	-	-	-	-
8	8	-	-	4	1	3	1	-	-	-	-	-	-	-
9	8	-	-	1	2	2	2	-	-	-	-	-	-	-
11 *	12/15	-	-	6/5	1/2	1/3	1/2	-	-	-	-	-	-	-
12	12	-	-	5	1	-	-	-	-	-	-	-	-	-
15*	2	-	-	20	-	15	3	-	-	-	-	-	-	-

Appendix 6.1: (Continued)

Date	Release Distance	Beetles released:									
		<u>N. brevicollis</u>		<u>P. madidus</u>		<u>Abax parallelepipedus</u>		<u>P. niger</u>		<u>C. violaceus</u>	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Aug 17	12			10	-	7	3	6	4	-	-
18	8			6	1	1	2	9	7	-	1
19	4			3	-	2	1	7	1	-	2
22*	12			10	-	3	1	10	9	1	1
23	15			3	1	-	1	1	3	-	-
24	12			3	1	1	1	-	1	-	1
25	12			1	1	1	-	12	10	-	1
26	12			1	1	1	1	3	7	-	-
29*	4		1	14	1	-	1	2	7	-	-
30	12		-	7	1	-	-	3	7	-	-
31	12		-	6	1	1	-	3	3	-	-
Sept 1	8		-	1	-	1	-	1	5	-	-
2	2		-	4	-	-	-	8	7	-	-
5*	4		1	1	-	-	-	10	10	-	-
6	8		2	1	-	1	-	1	2	-	-
7	12		2	1	-	-	-	1	3	-	-
8	15		2	5	-	-	-	2	2	-	-
9	2		2	4	-	-	-	4	2	-	-
12*	8		4	8	3	1	2	3	5	-	-
13	4		4	-	3	-	-	6	6	-	-
14	12		-	1	3	-	-	1	1	-	-
15	15		-	1	1	-	-	2	4	-	-
16	12		1	4	1	-	1	2	2	-	-
19*	4		3	6	1	-	1	1	1	-	-
20	12		6	4	4	-	-	1	1	-	-
21	2		2	6	4	-	-	1	1	-	-
22	1		4	2	-	-	-	1	1	-	-
23	12		18	6	1	1	-	1	1	-	-

Appendix 6.1: (Continued)

Date	Release Distance	Beetles released:											
		<u>N. brevicollis</u>		<u>P. madidus</u>		<u>Abax parallelepipedus</u>		<u>P. niger</u>		<u>C. violaceus</u>			
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		
Sept 26*	1	41	21	2	9	-	-	-	-	-	-	-	-
27	15	29	13	-	5	-	-	-	-	-	-	-	-
28	4	31	18	1	7	-	-	-	-	-	-	-	-
29	2	15	10	-	4	-	-	-	-	-	-	-	-
30	8	14	10	2	1	-	-	-	-	-	-	-	-
Oct 2*	12	18	13	-	7	-	-	-	-	-	-	-	-
4*	2	33	15	2	3	-	-	-	-	-	-	-	-
5	8	25	4	-	2	-	-	-	-	-	-	-	-
6	15	29	7	-	3	-	-	-	-	-	-	-	-
7	4	47	10	-	3	-	-	-	-	-	-	-	-
10*	12	41	11	-	8	-	-	-	-	-	-	-	-
12*	8	20	10	-	7	-	-	-	-	-	-	-	-
13	1	9	2	-	4	-	-	-	-	-	-	-	-
14	2	15	9	-	4	-	-	-	-	-	-	-	-
17*	1	48	13	1	10	-	-	-	-	-	-	-	-
19*	2	31	11	2	16	-	-	-	-	-	-	-	-
20	15	20	8	-	4	-	-	-	-	-	-	-	-
21(23)*	1	22	9	-	13	-	-	-	-	-	-	-	-
24*	8	71	30	1	12	-	-	-	-	-	-	-	-
26*	15	19	14	-	7	-	-	-	-	-	-	-	-
27(28)*	1	7	8	-	5	-	-	-	-	-	-	-	-
28	12	10	-	-	6	-	-	-	-	-	-	-	-
31*	4	26	13	1	9	-	-	-	-	-	-	-	-
Nov 1	4	5	1	-	1	-	-	-	-	-	-	-	-
2	4	9	2	-	3	-	-	-	-	-	-	-	-
3	12	18	6	-	4	-	-	-	-	-	-	-	-
4	12	2	2	-	4	-	-	-	-	-	-	-	-
8(9)*	1	29	9	-	7	-	-	-	-	-	-	-	-

no further captures until next April

no further captures until next May

no further captures

Appendix 6.1: (Continued)

Date	Release Distance	Beetles released:									
		<u>N. brevicollis</u>		<u>P. madidus</u>		<u>Abax parallelepipedus</u>		<u>P. niger</u>		<u>C. violaceus</u>	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Mar 20*	2	3	2	1	4						
21	8	1	3	-	-						
22(23)*	1	-	-	-	-						
23	12	1	1	-	2						
28*	1	3	1	-	1						
29	8	4	4	-	1						
30(31)	-	-	-	-	-						
31	12	1	-	-	-						
Apr 3*	12	7	3	3	6	-	-	-	-	-	-
4	4	-	-	-	1	1					
5	2	1	-	-	-						
7*	-	-	-	-	-						
10*	4	2	-	-	1						
12*	-	-	-	-	-						
13	-	-	-	-	-						
14	1	-	1	-	-						
15	-	-	-	-	-						
16(17)*	-	-	-	-	-						
17	8	-	-	2	-						
18	-	-	-	-	-						
19	8	-	-	1	1						
20	4	-	-	-	-						
21	15	1	-	-	1						
22	1	-	-	-	3						
24*	2	-	-	-	2						
25	8	-	1	4	4						
26	15	-	-	2	2						

Appendix 6.1: (Continued)

Date	Release Distance	Beetles released:												
		<u>N. brevicollis</u>		<u>P. madidus</u>		<u>Abax parallelepipedus</u>		<u>P. niger</u>		<u>C. violaceus</u>				
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀			
June 5	2	2	1	2	6	5	2	-	1	-	-	-	-	-
6	4	5	1	4	6	10	1	-	1	-	1	-	1	-
7	8	-	2	3	6	5	4	-	1	-	4	-	1	-
8	12	4	3	2	4	16	2	-	5	-	5	-	1	-
9	15	6	4	4	9	11	2	-	2	-	2	-	1	-
10	20	2	4	4	4	6	4	-	4	-	4	-	1	-
11	12	2	3	5	11	1	1	-	1	-	1	-	-	-
12	2	2	1	2	5	4	4	-	4	-	3	-	-	-
13	1	1	-	10	1	1	3	-	1	-	1	-	-	-
14	1	-	-	5	3	3	2	-	1	-	1	-	-	-
15	1	3	2	2	7	2	8	-	1	-	1	-	-	-
16	1	1	1	4	1	8	3	-	1	-	3	-	1	-
17	1	5	2	8	3	3	3	-	3	-	2	-	-	-
19*	1	1	1	14	6	11	2	-	1	-	2	-	4	-
20	2	2	-	13	3	12	3	-	1	-	3	-	-	-
21	4	-	1	9	4	5	4	-	1	-	4	-	1	-
23*	8	-	3	9	4	15	3	-	2	-	2	-	2	-
25*	12	1	1	8	4	5	3	-	3	-	3	-	-	-
26	15	1	1	6	1	6	1	-	1	-	1	-	1	-
28*	15	1	1	9	-	5	3	-	3	-	3	-	1	-
29(30)*	1	-	-	3	1	3	1	-	1	-	1	-	-	-

Appendix 6.2: Recapture records for *Nebria brevicollis* adults :
enlarged grid 1977-78

(Abbreviations are as follows: DRC date of recapture; DRL date of release; IM individual code mark; SRL site of release; DD direction of displaced release point (see below); SRC site of recapture; d(t) distance between respective traps,(m); d(b) actual nett displacement achieved by beetle (m); t time interval between captures (days).

* refers to those catches where the beetles were not removed from the traps on the day following capture, and hence the time interval cannot be precisely determined. DD: eight displacements were used and coded according to angle in relation to prominent features of the study site, i.e. P refers to direction of the pine plantation, R to the Council Refuse Tip, O to the oakwood itself, and F to the field adjacent - combinations of letters refer to the angle between the two features. The final column is used to indicate whether the beetle is known to have overwintered or is part of the new generation of adults, where known).

(i) Beetles released at 1m distance from the source trap

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
13.vi	7.vi	1/342	♀	E2	F	E2	-	1	*
26.ix	22.ix	1/467	♂	G5	R	H3	34	33	*
2.x	22.ix	1/468	♂	G7	FP	G5	30	29	*
13.x	22.ix	1/465	♂	B3	O	B3	-	1	21
14.x	13.x	1/465	♂	B3	F	C3	15	16	1
17.x	13.x	1/883	♂	E1	R	E1	-	1	*
17.x	13.x	1/781	♂	G10	PR	E10	15	16	*
17.x	13.x	1/862	♂	B8	RO	G8	75	74	*
19.x	13.x	1/884	♂	E9	P	E3	90	89	*
10.xi	9.xi	2/434	♂	A7	F	A7	-	1	1
11.xi	10.xi	2/434	♂	A7	FP	A7	-	1	1
14.xi	10.xi	1/554	♂	E7	PR	E7	-	1	*
21.iii	15.iii	2/505	♀	C5	FP	C5	-	1	6

Appendix 6.2: (Continued)

(ii) Beetles released at 2m distance from the source trap (cont)

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
13.ix	9.ix	1/409	♀	A7	RO	A7	-	2	4
30.ix	29.ix	1/654	♂	C7	PR	C7	-	2	1
30.ix	29.ix	1597	♂	F6	R	F6	-	2	1 O/W
30.ix	29.ix	1/662	♂	H7	P	H7	-	2	1
2.x	29.ix	1/657	♂	F6	R	F6	-	2	*
2.x	21.ix	1/461	♀	H6	P	G5	21	20	*
2.x	29.ix	1/664	♀	H8	OF	G9	21	19	*
5.x	29.ix	1/658	♂	F6	R	C4	56	55	6
7.x	29.ix	1/445	♀	C7	PR	C7	-	2	8
7.x	21.ix	1/462	♂	H7	RO	E3	75	77	16
7.x	29.ix	1812	♂	G7	R	G7	-	2	8 O/W
12.x	29.ix	1/656	♀	F6	R	B9	75	77	13
12.x	29.ix	1/653	♀	A7	O	C9	42	41	13
12.x	29.ix	1/659	♀	G2	P	G2	-	2	13
12.x	29.ix	1936	♂	H7	P	H7	-	2	13 O/W
17.x	14.x	1/273	♂	C7	FP	C7	-	2	* O/W
17.x	14.x	1/890	♂	C7	FP	C7	-	2	*
17.x	14.x	1/609	♂	C8	PR	C8	-	2	*
17.x	14.x	1/751	♂	E1	R	E1	-	2	*
17.x	14.x	1/892	♂	E1	R	E1	-	2	*
19.x	14.x	1/889	♀	C5	PR	D3	34	33	*
19.x	14.x	1/887	♂	A7	O	E7	60	61	*
20.x	14.x	1827	♀	C7	FP	C6	15	13	6 O/W
21.x	14.x	1/895	♀	F6	P	G5	21	20	7
24.x	29.ix	1/485	♂	F8	F	C7	48	47	*
24.x	14.x	1/549	♀	F8	F	C7	48	47	*
24.x	14.x	1/896	♀	F7	FP	C7	45	44	*
24.x	14.x	1/894	♀	F4	PR	F4	-	2	*
24.x	14.x	1/767	♂	F5	PR	H7	42	42	*
31.x	14.x	1/888	♀	B9	RO	B8	15	17	*
31.x	14.x	1/591	♂	F8	F	C7	48	46	*
31.x	14.x	1/719	♂	G4	OF	H7	48	47	*
10.xi	14.x	1/876	♂	G5	F	G4	15	15	27
11.xi	4.xi	1/837	♂	G5	F	G5	-	2	7
10.iv	5.iv	1/876	♂	F5	FP	F5	-	2	*

Appendix 6.2: (Continued)

(iii) Beetles released at 4m distance from the source trap

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.ix	13.ix	1/426	♀	A7	O	A7	-	4	3
29.ix	28.ix	1/615	♂	B6	RO	C7	21	17	1
29.ix	28.ix	1/624	♂	E3	R	E3	-	4	1
29.ix	28.ix	1/485	♂	F10	RO	F8	30	33	1
30.ix	28.ix	1/609	♂	A4	P	C5	34	36	2
2.x	13.ix	1/425	♀	A7	O	A5	30	34	*
2.x	28.ix	1/627	♂	E4	RO	E7	45	42	*
2.x	28.ix	1/587	♂	G9	RO	G9	-	4	*
4.x	28.ix	1016	♂	G5	F	G5	-	4	6 O/W
4.x	28.ix	1/640	♂	H9	RO	G7	34	37	6
7.x	28.ix	1/629	♂	F4	O	F4	-	4	9
7.x	28.ix	1879	♂	G5	F	G2	45	45	9 O/W
10.x	28.ix	1/614	♂	B6	RO	B6	-	4	*
10.x	28.ix	1/616	♀	B9	R	B8	15	16	*
10.x	7.x	1/796	♂	C8	FP	B9	15	16	*
10.x	7.x	1812	♂	G7	OF	B9	81	77	* O/W
10.x	7.x	1/794	♂	C4	FP	C4	-	4	*
10.x	7.x	1/765	♂	C8	FP	C8	-	4	*
10.x	7.x	1/808	♀	F8	R	E7	21	24	*
10.x	7.x	1/734	♂	G10	FP	F8	34	30	*
10.x	28.ix	1/527	♂	G2	PR	G2	-	4	*
10.x	7.x	1/810	♂	G4	RO	G4	-	4	*
10.x	7.x	1/467	♂	G5	RO	G5	-	4	*
10.x	28.ix	1/634	♂	G8	P	G5	45	41	*
10.x	7.x	1/733	♂	F8	R	G8	15	11	*
10.x	7.x	1/627	♂	E7	O	G8	31	32	*
10.x	7.x	1/354	♂	H9	F	H9	-	4	*
12.x	7.x	1/749	♂	B9	FP	B9	-	4	5
12.x	28.ix	1/513	♂	E1	R	E4	45	45	14
12.x	7.x	1/800	♂	E4	PR	E4	-	4	5
12.x	28.ix	1/630	♀	F7	R	E8	21	24	14
12.x	7.x	1/815	♂	H7	OF	H7	-	4	5
13.x	7.x	1/801	♂	E4	PR	E4	-	4	6
13.x	7.x	1/462	♂	E3	FP	E4	15	18	6
13.x	7.x	1/781	♂	G10	FP	G10	-	4	6
13.x	7.x	1/719	♂	F5	P	G4	21	19	7
17.x	7.x	1/711	♂	B9	FP	A7	34	30	*
17.x	28.ix	1/628	♀	E5	PR	E8	45	48	*
17.x	7.x	1/629	♂	F4	P	F4	-	4	*
17.x	7.x	1/455	♂	A7	PR	F7	75	72	*
17.x	7.x	1/802	♂	E5	R	F8	48	47	*
19.x	28.ix	1/508	♀	B9	R	B9	-	4	*
19.x	28.ix	1/519	♀	F7	R	C9	54	57	*
19.x	7.x	1/773	♂	E3	FP	E1	30	27	*
20.x	7.x	1/595	♂	E7	O	E7	-	4	13

Appendix 6.2: (Continued)

(iii) Beetles released at 4m distance from the source trap (cont)

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
21.x	7.x	1/795	♀	C4	FP	B4	15	12	14
21.x	28.ix	1/620	♀	E2	PR	H4	54	54	23
24.x	7.x	1/816	♂	H7	OF	C4	87	87	*
24.x	28.ix	1/623	♂	E3	R	C4	34	37	*
24.x	28.ix	1/632	♀	G4	P	G5	15	19	*
24.x	7.x	1/804	♂	E7	O	G7	30	30	*
26.x	7.x	1/803	♂	E7	O	B9	54	52	*
27.x	7.x	1/712	♂	A9	F	B9	15	19	20
31.x	7.x	1/792	♀	B9	FP	C6	48	46	24
31.x	7.x	1/814	♂	G10	FP	C7	75	71	*
31.x	7.x	1/702	♀	H8	F	H7	15	16	*
2.xi	1.xi	2/321	♂	F9	OF	G9	15	18	1
3.xi	1.xi	2/393	♂	E1	RO	E1	-	4	2
8.xi	1.xi	1/492	♂	C6	RO	A7	34	35	*
29.xi	1.xi	2/395	♂	H7	P	H7	-	4	*

(iv) Beetles released at 8m distance from the source trap

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.ix	6.ix	1/398	♂	G2	RO	G5	45	39	10
2.x	30.ix	1/683	♂	G10	RO	G9	15	22	*
4.x	30.ix	1/654	♂	C7	R	C7	-	8	4
4.x	30.ix	1597	♂	F6	RO	F7	15	11	4 O/W
6.x	5.x	1/480	♂	E4	FP	E4	-	8	1
6.x	30.ix	1/682	♂	G10	RO	G10	-	8	6
7.x	5.x	1/750	♀	B9	OF	A9	15	11	2
7.x	5.x	1/749	♂	B9	OF	B9	-	8	2
7.x	5.x	1/235	♂	G9	OF	F9	15	11	2 O/W
7.x	30.ix	1/467	♂	G5	FP	G5	-	8	7
7.x	5.x	1/734	♂	G10	OF	G10	-	8	2
12.x	5.x	1/658	♂	C4	OF	F8	75	74	7
14.x	30.ix	1/609	♂	C5	FP	C8	45	51	14
14.x	5.x	1/751	♂	E1	OF	E1	-	8	9
14.x	5.x	1/727	♂	G4	R	H6	34	31	9
17.x	30.ix	798	♂	E9	FP	F8	21	23	* O/W
19.x	5.x	1/310	♂	B8	P	C10	34	41	*
20.x	30.ix	1/487	♀	E9	FP	E9	-	8	20
24.x	30.ix	1/532	♂	G5	FP	C4	62	55	*
24.x	30.ix	1/673	♀	E4	O	E4	-	8	*
24.x	30.ix	1/672	♀	E2	R	F4	34	31	*
24.x	5.x	1/707	♂	C4	OF	G5	62	66	*

Appendix 6.2: (Continued)

(iv) Beetles released at 8m distance from the source trap (cont).

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
24.x	5.x	1/757	♂	G4	R	G7	45	46	*
24.x	5.x	1/356	♂	E7	R	G9	42	38	*
29.iii	14.iii	2/493	♂	B2	RO	B5	45	39	15
29.iii	21.iii	2/505	♀	C5	PR	C5	-	8	8
3.iv	21.iii	2/509	♀	H3	FP	E4	48	44	*

(v) Beetles released at 12m distance from the source trap

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.ix	7.ix	1/403	♀	H10	F	E8	54	45	9
19.ix	16.ix	1/398	♂	G5	P	G4	15	3	*
26.ix	16.ix	1/435	♀	A1	OF	B1	15	24	*
26.ix	16.ix	1/426	♀	A7	F	B3	62	66	*
26.ix	23.ix	1/481	♂	E4	P	E4	-	12	*
28.ix	23.ix	1/473	♂	A7	PR	A7	-	12	5
28.ix	16.ix	1/403	♀	E8	R	E8	-	12	12
28.ix	23.ix	1/485	♂	G8	OF	F10	34	22	5
29.ix	23.ix	1/297	♂	A7	PR	A7	-	12	6 N/G
30.ix	23.ix	1/484	♀	G9	P	E9	30	32	7
2.x	23.ix	1/479	♀	C6	OF	A7	34	23	*
2.x	16.ix	1/437	♂	E7	R	A7	60	72	*
4.x	23.ix	1/480	♂	E3	P	E4	15	27	11
5.x	20.ix	1/310	♂	A7	P	B8	21	31	15
7.x	20.ix	1/455	♂	B9	FP	A7	34	22	17
10.x	23.ix	1/478	♂	B9	P	C4	76	65	*
19.x	23.ix	1/483	♀	E8	RO	E9	15	11	*
21.x	23.ix	1/444	♂	A7	PR	E7	60	53	28
3.xi	2.xi	1/564	♂	C4	OF	C4	-	12	1
3.xi	28.x	2/374	♂	E1	PR	E1	-	12	6
3.xi	2.xi	2/308	♀	E1	O	E4	45	33	1
4.xi	3.xi	2/401	♂	C5	RO	C7	30	22	1
4.xi	2.xi	1/465	♂	H3	OF	H4	15	11	2
8.xi	2.xi	2/380	♂	B9	O	E6	64	56	*
8.xi	28.x	798	♂	H7	F	E7	45	33	* O/W
8.xi	3.xi	1/956	♂	G10	R	G7	45	47	*
10.xi	3.xi	1/626	♂	A7	O	A7	-	12	7
10.xi	3.xi	1/963	♂	C9	RO	E7	42	44	7
10.xi	3.xi	1/916	♂	E7	FP	E7	-	12	7
10.xi	3.xi	1/689	♂	D4	O	G4	45	47	7
14.xi	28.x	2/375	♂	F8	OF	E7	21	24	*
14.xi	3.xi	1/845	♂	G5	P	F8	48	59	*
14.xi	28.x	1/751	♂	E1	PR	G2	34	32	*
15.xi	3.xi	1/830	♀	C4	F	C4	-	12	12
30.i	24.i	1/657	♂	E6	OF	D6	15	11	*

Appendix 6.2 (Continued)

(vi) Beetles released at 15m distance from the source trap

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.ix	8.ix	1/407	♀	F8	R	G9	21	15	8
28.ix	27.ix	1/579	♂	E2	P	E1	15	1	1
28.ix	27.ix	1/587	♂	E8	OF	G9	34	41	1
28.ix	27.ix	1/600	♂	G9	R	G9	-	15	1
29.ix	27.ix	1/584	♂	E7	F	F8	21	34	2
30.ix	27.ix	1/526	♀	H4	F	G8	34	30	3
2.x	27.ix	1/571	♂	C5	F	B5	15	1	*
2.x	27.ix	1/585	♂	E7	F	E7	-	15	*
4.x	27.ix	1/598	♂	G7	PR	E4	54	53	7
4.x	27.ix	1/568	♂	A4	FP	E3	62	71	7
6.x	27.ix	1/586	♂	E7	F	B9	54	42	9
7.x	6.x	1/712	♀	B9	F	A9	15	1	1
7.x	6.x	1/767	♂	C4	F	B4	15	1	1
7.x	6.x	1/711	♂	B9	F	B9	-	15	1
7.x	6.x	1/765	♂	B9	F	C8	21	34	1
7.x	6.x	1/773	♂	E4	P	E3	15	1	1
7.x	6.x	1/502	♂	E4	P	E4	-	15	1
7.x	27.ix	1/595	♂	G5	OF	E7	42	27	10
7.x	6.x	1/733	♂	H9	OF	F8	34	32	1
7.x	6.x	1/780	♂	G8	RO	F9	21	26	1
7.x	6.x	1/682	♂	G10	F	F10	15	1	1
6.x	6.x	1/781	♂	G10	F	G10	-	15	1
10.x	6.x	1/767	♂	C4	F	B4	15	1	*
10.x	6.x	1/533	♂	E7	RO	C7	30	42	*
10.x	6.x	1/770	♂	E1	F	E1	-	15	*
10.x	6.x	1/480	♂	E4	P	E3	15	1	*
12.x	6.x	1/775	♀	E4	P	E5	15	30	6
13.x	6.x	1/771	♀	E3	F	G7	67	75	7
14.x	6.x	1/591	♂	F8	OF	F8	-	15	17
17.x	6.x	1/774	♂	E4	P	A3	62	60	*
17.x	6.x	1/788	♀	F6	F	D9	54	48	*
17.x	27.ix	1/581	♂	E4	R	H6	54	42	*
17.x	27.ix	1/593	♂	G5	OF	H7	34	32	*
17.x	6.x	1/784	♂	H9	OF	H9	-	15	*
19.x	27.ix	1/582	♂	E7	F	E7	-	15	*
21.x	20.x	1/900	♂	C7	R	A7	30	45	1
21.x	20.x	1/824	♂	B10	F	B9	15	21	1
21.x	27.ix	1422	♂	F7	PR	E9	34	48	24 O/W
24.x	20.x	1/962	♀	A6	O	A7	15	1	*
24.x	20.x	1/965	♂	D6	FP	C7	21	26	*
24.x	20.x	1/968	♂	E1	OF	E1	-	15	*
24.x	20.x	1/773	♂	E1	OF	E3	30	24	*
24.x	6.x	1/375	♂	H7	O	H6	15	30	*
26.x	20.x	1/963	♂	A7	F	B9	34	42	*
26.x	20.x	1/487	♀	E9	R	H9	45	30	*
28.x	6.x	1/716	♀	D1	PR	G2	48	43	22

Appendix 6.2 (Continued)

(vi) Beetles released at 15m distance from the source trap (cont).

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
31.x	20.x	1/959	♂	H7	R	H7	-	15	*
2.xi	20.x	1/710	♂	F8	PR	H7	34	20	13
3.xi	20.x	1/845	♂	H5	R	G5	15	30	14
8.xi	20.x	1/973	♂	G5	PR	B5	75	87	*
8.xi	20.x	1/971	♂	F7	R	H7	30	15	*
10.xi	20.x	1827	♀	C6	FP	C5	15	7	21 O/W
14.xi	11.xi	2/448	♂	H2	OF	G4	34	19	*
14.xi	11.xi	1/837	♂	G5	P	G4	15	1	*
14.xi	20.x	1/629	♂	E4	P	H7	64	75	*
15.xi	11.xi	1/673	♀	G5	P	H3	34	21	4
30.i	24.i	2/483	♀	H6	FP	G6	15	12	*

Appendix 6.3: Recapture records for Pterostichus madidus adults :
enlarged grid 1977-78.

(Abbreviations as per Appendix 6.2)

(i) Beetles released at 1m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
31.v	30.v	2/514	♀	E6	FP	E6	-	1	1 O/W
2.vi	30.v	2/524	♀	F4	P	F4	-	1	* O/W
6.vi	2.vi	2/550	♀	B9	PR	B9	-	1	* O/W
6.vi	31.v	2/547	♀	F4	PR	F4	-	1	* O/W
9.vi	27.v	2/491	♀	C1	FP	C1	-	1	13 O/W
16.vi	2.vi	2/555	♀	E6	PR	E6	-	1	14 O/W
20.vi	9.vi	2/491	♀	C1	R	C1	-	1	* O/W
21.vi	20.vi	2/611	♀	E2	P	E2	-	1	1 O/W
26.vi	30.v	2/535	♀	F4	P	F4	-	1	* O/W
29.vi	26.vi	2/663	♂	D1	RO	D1	-	1	* O/W
30.vi	29.vi	2/677	♂	B4	R	C4	15	14	1 O/W
27.vii	29.vi	2/700	♂	G3	R	E1	42	43	28 O/W
11.viii	8.viii	2/688	♂	E8	OF	E7	15	16	* O/W
23.viii	8.viii	2/837	♂	G8	FP	G9	15	16	15
27.ix	26.ix	3/428	♀	G2	FP	G2	-	1	1
27.ix	26.ix	3/429	♀	G3	OF	G3	-	1	1
2.x	26.ix	3/422	♀	A5	R	A5	-	1	*
19.x	17.x	3/496	♀	B9	O	B9	-	1	*
19.x	17.x	3/497	♀	C10	RO	C10	-	1	*
2.xi	23.x	3/530	♀	B8	OF	A8	15	14	10

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
13.v	12.v	2/377	♂	C6	PR	C6	-	2	1 O/W
13.v	12.v	2/359	♂	D8	P	D8	-	2	1 O/W
16.v	12.v	2/373	♀	B3	P	B3	-	2	* O/W
16.v	13.v	2/377	♂	C6	R	C6	-	2	* O/W
15.vi	13.vi	2/586	♂	C4	P	C4	-	2	2 O/W
1.vii	15.vi	2/600	♂	D3	P	E3	15	16	16 O/W
22.viii	15.viii	2/875	♂	B9	R	B8	15	16	*
17.x	29.ix	3/447	♀	F4	OF	F4	-	2	*
24.x	14.x	3/491	♀	D5	P	B8	54	55	*
23.iii	20.iii	3/623	♀	H4	PR	H4	-	2	3

Appendix 6.3: (Continued)

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
23.v	20.v	2/431	♀	H7	P	H7	-	4	* O/W
6.vi	16.v	2/390	♀	D8	R	D8	-	4	* O/W
11.i	21.xii	2/966	♀	B5	FP	E8	64	68	21

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
6.viii	2.viii	2/806	♂	E3	O	E6	45	37	*
3.xi	24.x	3/550	♀	F5	RO	C4	47	54	10

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
29.viii	25.viii	2/936	♂	G3	OF	F4	21	9	*
26.ix	20.ix	2/398	♀	H5	OF	H5	-	12	* O/W
6.x	2.x	3/454	♀	E8	FP	E8	-	12	4
31.x	10.x	3/476	♀	G2	OF	F2	15	10	*
8.xi	28.x	3/572	♀	F5	O	F6	15	3	*

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
29.vii	25.vii	2/779	♂	G1	R	H1	15	1	4
6.viii	25.vii	2/766	♂	A10	O	A10	-	15	*
11.viii	25.vii	2/775	♂	E10	PR	E8	30	22	*
15.viii	11.viii	2/854	♂	F4	OF	F6	30	22	*
22.viii	11.viii	2/688	♂	E7	OF	D6	21	26	* O/W
12.ix	8.ix	2/984	♂	B4	O	B4	-	15	*
24.x	6.x	3/454	♀	E8	P	H6	54	47	*
20.iii	10.iii	3/576	♂	C5	OF	B7	34	19	*

Appendix 6.4: Recapture records for *Abax parallelepipedus* adults:
enlarged grid 1977-78.

(Abbreviations as per Appendix 6.2)

(i) Beetles released at 1m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
6.vi	30.v	158	♂	H4	-	H4	-	1	*
29.vi	30.v	523	♂	H4	-	H4	-	1	*
30.vi	29.vi	568	♂	F7	-	F7	-	1	1

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
17.viii	15.viii	650	♂	D10	-	D10	-	2	2
12.ix	15.viii	651	♂	E3	-	E3	-	2	*

(iii) Beetles released at 4m

none recaptured

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
22.viii	9.viii	636	♂	G7	R	C6	62	70	*
29.viii	18.viii	671	♀	A8	F	A8	-	8	*

(v) Beetles released at 12m

none recaptured

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
6.viii	25.vii	463	♀	E2	F	D2	15	1	12

Appendix 6.5: Recapture records for Pterostichus niger adults:enlarged grid 1977-78

(Abbreviations as per Appendix 6.2)

(i) Beetles released at 1m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
17.viii	7.viii	88	♀	G9	PR	D9	45	45	10
18.viii	8.viii	93	♀	C4	P	B5	21	22	10

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
17.viii	15.viii	125	♀	A10	P	A10	-	2	2
19.viii	15.viii	148	♂	H7	R	H7	-	2	4
25.viii	15.viii	147	♂	H7	R	D6	62	64	10
25.viii	15.viii	142	♂	E8	FP	F6	34	33	10
26.viii	15.viii	136	♂	D7	R	F3	67	66	11
30.viii	15.viii	137	♂	E3	PR	F2	21	19	15
31.viii	15.viii	131	♂	B7	RO	F3	85	85	16
1.ix	15.viii	122	♂	A6	RO	D6	45	44	17
5.ix	2.ix	252	♀	A7	FP	A7	-	2	*
5.ix	15.viii	146	♂	G7	O	A8	91	91	*
5.ix	15.viii	124	♂	A8	OF	C8	30	31	*
7.ix	15.viii	133	♀	C4	PR	D7	48	48	21
8.ix	15.viii	144	♂	F6	P	A6	75	75	24
9.ix	15.viii	145	♀	G7	O	G6	15	17	25

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
15.viii	1.viii	69	♀	E6	FP	F6	15	18	*
18.viii	28.vii	66	♀	H5	P	H6	15	19	21
22.viii	19.viii	148	♂	H7	OF	H7	-	4	*
25.viii	28.vii	65	♀	C4	F	E3	34	37	28
25.viii	1.viii	70	♀	G2	RO	F3	21	22	24
5.ix	29.viii	234	♀	B9	OF	A4	76	79	*
7.ix	5.ix	73	♀	C4	R	B6	34	36	2
12.ix	29.viii	226	♀	F3	OF	E6	48	44	*
14.ix	5.ix	170	♂	F3	P	F3	-	4	9
15.ix	5.ix	146	♂	A8	O	A6	30	34	10
16.ix	5.ix	261	♂	C6	R	D5	21	19	11
28.ix	13.ix	288	♀	F10	PR	F9	15	12	15

Appendix 6.5: (Continued)

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
15.viii	8.viii	91	♂	B5	PR	D3	42	34	*
15.viii	8.viii	101	♂	F6	F	E5	17	17	*
22.viii	18.viii	174	♂	G7	F	B6	76	69	*
22.viii	18.viii	171	♀	E3	RO	E5	30	25	*
22.viii	9.viii	104	♂	E5	PR	E5	-	8	*
22.viii	9.viii	105	♂	H8	P	H10	30	38	*
26.viii	2.viii	71	♀	C4	FP	F7	64	72	24
5.ix	18.viii	93	♀	B5	OF	A8	48	40	*
5.ix	18.viii	175	♂	H5	FP	F2	54	46	*
5.ix	18.viii	170	♂	E3	RO	F3	15	11	*
5.ix	18.viii	172	♂	E3	RO	H4	48	40	*
8.ix	9.ix	103	♂	E3	FP	F5	34	42	30

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
22.viii	17.viii	156	♂	A10	PR	A10	-	12	*
29.viii	26.viii	226	♀	D6	PR	F3	54	42	*
30.viii	26.viii	223	♂	A5	OF	A7	30	23	4
30.viii	24.viii	204	♀	A6	F	B5	21	31	6
31.viii	22.viii	184	♀	A4	R	C7	54	48	9
31.viii	17.viii	160	♀	E3	R	F3	15	3	14
1.ix	25.viii	209	♀	D7	OF	F9	42	44	7
2.ix	31.viii	246	♀	F3	F	A4	76	65	2
2.ix	22.viii	190	♂	C7	P	B7	15	19	11
2.ix	25.viii	213	♂	F3	RO	F3	-	12	8
2.ix	30.viii	241	♀	H3	F	H3	-	12	3
5.ix	25.viii	216	♀	F9	R	E5	62	66	*
12.ix	17.viii	125	♀	A10	PR	D10	45	38	*
12.ix	25.viii	65	♀	E3	OF	E5	30	23	*
12.ix	30.viii	239	♂	F2	O	F3	15	3	*
20.ix	25.viii	214	♂	F6	RO	H6	30	23	26
22.ix	20.ix	214	♂	H6	FP	F6	30	23	2

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
18.viii	11.viii	114	♂	G4	RO	H4	15	12	7
22.viii	11.viii	109	♂	C5	PR	E5	30	22	*
31.viii	23.viii	202	♀	B6	O	A9	47	34	8

Appendix 6.6: Recapture records for Carabus violaceus adults;
enlarged grid 1977-78

(Abbreviations as per Appendix 6.2)

(i) Beetles released at 1m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
27.vii	20.vii	61	♂	D5	FP	B5	30	29	7

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
14.vi	13.vi	55	♂	G4	RO	G4	-	2	1
22.viii	15.viii	61	♂	G4	OF	H6	34	34	7

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
28.vii	27.vii	61	♂	B5	F	B5	-	4	1
6.viii	27.vii	65	♀	B5	F	B5	-	4	10
6.viii	1.viii	64	♀	G4	P	D6	54	56	5
15.viii	28.vii	61	♂	B5	FP	G4	76	79	18

(iv) Beetles released at 8m

none recaptured

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
1.ix	12.viii	78	♀	G4	0	H2	34	45	20

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
1.viii	25.vii	64	♀	F3	FP	G4	21	36	7
19.viii	11.viii	76	♀	D8	RO	D10	30	22	8

Appendix 6.7: Recapture records for Nebria brevicollis adults:PX18 grid, Spring 1978.

(Abbreviations as per Appendix 6.2)

(i) Beetles released at 1m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
3.v	30.iv	2/521	♂	S1	O	Q3	14	13	3 O/W
6.v	30.iv	2/523	♀	X2	R	R1	26	26	6 O/W
8.v	30.iv	2/522	♀	T1	F	W8	36	37	8 O/W
16.v	30.iv	1/593	♂	Q8	OF	Q8	-	1	16 O/W
20.vi	26.v	2/536	♂	Q5	FP	R2	16	15	25 N/G
28.vi	16.vi	2/626	♂	W1	R	T4	18	19	*

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
30.iv	27.iv	1/593	♂	Q8	O	Q8	-	2	3 O/W
3.v	2.v	2/520	♂	W3	OF	X2	7	9	1 O/W
28.v	24.v	2/532	♂	Q8	OF	S5	18	20	* N/G

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
1.vi	31.v	2/552	♂	Q8	P	P7	7	5	1
2.vi	31.v	2/560	♀	W8	OF	W8	-	4	2 N/G
6.vi	31.v	2/562	♂	X3	OF	W1	11	13	6 N/G
7.vi	6.vi	2/593	♀	W8	P	W7	3	1	1 N/G
25.vi	21.vi	2/636	♀	W2	P	V5	16	19	*

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
6.vi	1.vi	2/568	♂	W1	O	W1	-	8	5 N/G

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	6.v	2/523	♀	R1	R	T2	11	5	* O/W
17.vi	8.vi	2/595	♀	P3	OF	R5	14	19	9 N/G

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
2.v	21.iv	2/520	♂	T1	RO	W3	14	1	11 O/W

Appendix 6.8: Recapture records for Pterostichus madidus adults :
PX18 Grid, 1978 (N.B. all beetles known to have over-
wintered 1977 to 1978).

(Abbreviations as per Appendix 6.2)

(i) Beetles released at lm

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
9.v	30.iv	3/682	♀	T1	F	Q2	16	15	9
9.v	8.v	3/757	♂	R1	RO	R1	-	1	1
10.v	8.v	3/776	♀	W2	P	W2	-	1	2
11.v	8.v	3/781	♀	X1	P	T1	15	15	3
22.v	8.v	3/764	♀	S8	F	S5	15	15	14
23.v	8.v	3/774	♀	V6	RO	T7	7	8	15
24.v	8.v	3/767	♀	T4	PR	T5	5	6	16
28.v	25.v	3/873	♀	S1	RO	S1	-	1	*
29.v	28.v	3/692	♀	R1	P	S2	7	8	1
29.v	26.v	3/885	♀	X3	RO	W4	7	7	3
31.v	8.v	3/768	♀	T5	F	P7	22	21	23
31.v	8.v	3/763	♀	S3	PR	S3	-	1	23
31.v	28.v	3/904	♀	V3	RO	S3	10	11	3
31.v	28.v	3/892	♀	R2	FP	T3	11	12	3
31.v	28.v	3/907	♀	W2	F	V2	5	4	3
2.vi	28.v	3/888	♀	Q1	O	P2	7	6	5
2.vi	28.v	3/893	♀	R3	O	S3	5	6	5
5.vi	8.v	3/773	♀	V6	RO	W6	5	4	28
6.vi	28.v	3/887	♂	P4	FP	P3	5	4	9
9.vi	28.v	3/908	♂	W3	RO	V3	5	6	12
9.vi	4.vi	3/705	♀	X2	P	W2	5	6	5
13.vi	28.v	3/869	♂	X7	R	V8	11	12	16
17.vi	29.v	3/692	♀	S2	RO	Q2	10	11	19
17.vi	28.v	3/886	♀	P3	PR	X2	36	35	20
19.vi	13.vi	4/535	♂	V7	PR	T2	26	26	*
19.vi	13.vi	4/536	♂	W2	OF	V4	11	10	*
20.vi	15.vi	3/943	♀	T1	RO	V1	5	4	5
20.vi	19.vi	4/574	♂	V5	P	V6	5	6	1
20.vi	15.vi	4/548	♀	W3	R	W3	-	1	5
21.vi	25.v	3/872	♀	R7	FP	P7	10	9	27
21.vi	15.vi	4/546	♀	T7	F	T7	-	1	6
21.vi	19.vi	4/573	♂	T4	P	V6	11	12	2
21.vi	17.vi	4/560	♂	X2	OF	W5	16	15	4
23.vi	19.vi	4/571	♂	S5	O	Q1	22	23	*
23.vi	19.vi	4/535	♂	T2	RO	V4	11	10	*
28.vi	17.vi	4/555	♂	P8	O	P4	20	21	*
29.vi	17.vi	4/557	♂	R4	RO	T1	18	18	12

Appendix 6.8: (Continued)

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	24.iv	3/655	♀	P2	P	R3	11	12	*
11.v	10.v	3/806	♀	Q7	PR	Q7	-	2	1
16.v	10.v	3/807	♀	R2	OF	T3	11	11	6
23.v	16.v	3/795	♀	S2	PR	W2	15	14	7
24.v	16.v	3/828	♀	S3	RO	R4	7	7	8
28.v	24.v	3/869	♂	X7	PR	X7	-	2	*
31.v	16.v	3/807	♀	T3	F	P3	20	18	15
4.vi	10.v	3/808	♀	R8	FP	P5	18	16	*
9.vi	5.vi	3/979	♀	W5	O	W4	5	7	4
9.vi	24.v	2/712	♀	R1	FP	R4	15	16	16
15.vi	24.v	3/828	♀	R4	F	R4	-	2	22
20.vi	24.v	3/868	♂	X3	PR	T1	18	18	27
23.vi	24.v	3/862	♀	Q6	F	P4	11	10	*
23.vi	20.vi	4/586	♂	W6	F	T2	22	21	*
23.vi	12.vi	4/529	♂	V5	FP	V4	5	4	*
25.vi	20.vi	3/868	♂	T1	O	V4	16	15	*

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.v	11.v	3/821	♀	V4	P	S3	11	10	5
22.v	4.v	3/771	♀	Q5	O	T1	25	28	18
23.v	4.v	3/721	♀	R2	R	T3	11	8	19
31.v	11.v	3/806	♀	Q7	R	R7	5	1	20
1.vi	11.v	3/811	♀	P7	RO	R8	11	7	21
1.vi	31.v	3/940	♀	R1	R	S1	5	1	1
4.vi	31.v	3/942	♀	R4	FP	Q3	7	3	*
7.vi	31.v	3/946	♀	X2	FP	W2	5	3	7
9.vi	11.v	3/820	♀	V1	F	V3	10	11	29
9.vi	31.v	3/798	♂	X4	RO	W2	11	15	9
11.vi	31.v	3/807	♀	P3	R	P1	10	11	11
15.vi	31.v	3/943	♀	S3	P	T1	11	8	15
21.vi	6.vi	3/984	♀	T5	FP	T5	-	4	15
23.vi	21.vi	4/590	♂	S7	F	S8	5	6	*
25.vi	31.v	3/892	♀	T3	O	T3	-	4	*
28.vi	21.vi	2/747	♂	T1	OF	V6	26	24	*
29.vi	31.v	3/944	♂	T5	F	P5	20	16	29
29.vi	21.vi	4/594	♂	X7	PR	V6	11	13	8

Appendix 6.8: (Continued)

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	25.iv	3/660	♂	T2	RO	V2	5	6	*
11.v	9.v	3/796	♀	V2	FP	T1	5	1	3
16.v	9.v	3/795	♀	V1	OF	S2	11	3	7
31.v	9.v	3/798	♂	W4	R	X4	5	3	22
4.vi	1.vi	3/954	♀	T3	OF	S3	5	6	*
9.vi	1.vi	3/949	♀	P2	RO	S3	16	9	8
19.vi	7.vi	3/993	♂	X3	F	T2	16	9	*
25.vi	23.vi	4/529	♂	V4	FP	T3	7	1	*
29.vi	23.vi	4/596	♀	P4	OF	P3	5	13	6

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
23.v	22.v	3/632	♀	Q2	O	S3	11	12	1
28.v	8.v	3/692	♀	V1	OF	R1	16	7	*
21.vi	11.vi	4/522	♂	W5	F	W4	5	13	10
23.vi	11.vi	3/643	♂	W4	OF	P1	34	34	*
23.vi	11.vi	4/514	♂	R2	OF	W6	28	29	*
26.vi	25.vi	4/529	♂	T3	FP	R1	14	2	1

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	26.iv	1/738	♂	T4	F	Q4	15	1	*
29.v	21.v	3/836	♀	T3	FP	V2	7	16	8
30.v	23.v	697	♀	T4	RO	V6	11	6	7
31.v	23.v	3/855	♀	T7	P	S1	31	16	8
2.vi	5.v	3/733	♀	W8	P	W5	15	1	28
4.vi	23.v	3/860	♀	W2	OF	T3	11	6	*
11.vi	9.vi	4/501	♀	R3	FP	R2	5	13	2
13.vi	9.vi	3/999	♂	P1	RO	X7	46	31	4
14.vi	23.v	3/858	♀	V7	F	S6	11	7	22
20.vi	9.vi	3/798	♂	W2	RO	S3	16	27	11
29.vi	28.vi	4/616	♂	V6	P	V3	15	1	1

(vii) Beetles released at 20m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	1.v	3/699	♂	V3	O	S7	27	11	*
8.v	1.v	3/692	♀	Q2	R	V1	21	7	*
23.v	1.v	3/709	♀	X5	FP	T5	15	12	22
21.vi	10.vi	2/747	♂	P2	P	T1	21	22	11

Appendix 6.9: Recapture records for Abax parallelepipedus adults:PX18 Grid, 1978

(Abbreviations as per Appendix 6.2)

(i) Beetles released at lm

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
24.v	8.v	730	♀	T7	OF	V8	7	7	16
29.v	28.v	776	♂	S3	FP	V1	14	14	1
4.vi	29.v	776	♂	V1	P	R2	16	16	*
4.vi	25.v	772	♂	X6	O	X7	5	4	*
5.vi	4.vi	790	♂	T6	FP	T7	5	6	1
6.vi	8.v	728	♂	S3	PR	P1	18	18	29
6.vi	26.v	774	♂	W5	R	S8	21	22	11
7.vi	29.v	716	♀	X4	PR	V1	18	18	9
8.vi	4.vi	806	♂	S3	R	R2	7	8	4
8.vi	29.v	754	♂	X5	O	R5	25	25	10
9.vi	28.v	778	♀	S7	PR	R7	5	6	12
12.vi	4.vi	763	♀	S6	PR	S6	-	1	8
12.vi	29.v	784	♂	X1	F	T1	15	14	14
12.vi	26.v	773	♀	V1	FP	V6	25	26	17
14.vi	4.vi	759	♂	S3	R	P2	16	17	10
15.vi	14.vi	857	♂	W2	F	W1	5	5	1
17.vi	16.vi	608	♂	T6	R	Q5	16	17	1
19.vi	13.vi	287	♂	Q1	RO	T1	15	14	*
20.vi	16.vi	860	♂	R8	O	S6	11	12	4
20.vi	19.vi	871	♂	X1	OF	X2	5	4	1
20.vi	19.vi	739	♂	X4	RO	X4	-	1	1
23.vi	19.vi	867	♂	P1	F	P2	5	5	*
23.vi	4.vi	785	♂	P6	OF	Q4	11	12	*
23.vi	19.vi	838	♂	R1	FP	R2	5	6	*
23.vi	16.vi	776	♂	Q1	OF	S4	18	18	*
23.vi	29.v	783	♂	V3	O	X7	22	21	*
26.vi	13.vi	716	♀	V6	O	T5	7	8	13
26.vi	19.vi	870	♂	T4	P	T5	5	6	7
26.vi	4.vi	811	♂	X4	F	X5	5	5	22
28.vi	4.vi	809	♂	V8	RO	Q7	21	22	*
29.vi	14.vi	759	♂	P2	RO	T1	21	21	15
29.vi	19.vi	829	♂	T4	P	V3	7	6	10
29.vi	17.vi	866	♀	W3	RO	V3	5	6	12
29.vi	4.vi	534	♀	W1	F	X6	26	26	25

Appendix 6.9: (Continued)

(ii) Beetles released at 2m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
8.v	3.v	714	♂	W1	FP	W2	5	7	*
16.v	24.iv	706	♂	V7	OF	S1	32	33	22
21.v	10.v	738	♂	S3	R	P5	18	20	11
21.v	16.v	745	♂	W6	FP	V8	11	12	5
22.v	2.v	713	♂	S1	F	T7	31	32	20
26.v	24.v	521	♂	R2	F	Q1	7	6	2
26.v	16.v	743	♀	W3	FP	W3	-	2	10
30.v	2.v	684	♀	T4	P	R1	18	16	28
30.v	24.v	730	♀	V8	FP	T6	11	9	6
1.vi	24.v	769	♂	X3	PR	R3	20	21	8
1.vi	24.v	722	♂	X4	FP	S2	22	20	8
1.vi	30.v	730	♀	T6	OF	S7	7	5	2
2.vi	30.v	785	♂	P7	OF	P6	5	6	3
4.vi	30.v	790	♂	V8	PR	T6	11	11	*
4.vi	16.v	656	♂	V8	OF	T8	5	4	*
6.vi	30.v	787	♂	R6	P	S8	11	13	7
8.vi	5.vi	817	♂	R8	F	R8	-	2	3
8.vi	30.v	788	♂	S2	O	S3	5	3	9
8.vi	24.v	745	♂	R7	F	S8	7	9	15
8.vi	5.vi	732	♀	V4	RO	V2	10	11	3
9.vi	5.vi	208	♂	V6	P	Q5	21	20	4
12.vi	30.v	684	♀	R1	PR	T1	10	9	13
19.vi	30.v	792	♂	X3	O	T6	21	20	*
23.vi	5.vi	790	♂	T7	PR	R8	11	13	*
23.vi	30.v	791	♂	W2	P	W1	5	3	*
25.vi	20.vi	860	♂	S6	FP	S8	10	12	*
26.vi	5.vi	815	♂	P3	RO	R6	18	16	21
28.vi	12.vi	854	♀	R2	F	V2	15	17	*
28.vi	20.vi	788	♂	X1	F	X2	5	6	*
29.vi	20.vi	871	♂	X2	F	V5	18	17	9

(iii) Beetles released at 4m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
6.v	4.v	715	♂	S4	OF	T6	11	11	2
23.v	4.v	717	♂	X1	F	W3	11	10	19
29.v	4.v	716	♀	W1	OF	X4	16	14	25
7.vi	31.v	796	♀	S6	FP	R8	11	13	7
7.vi	6.vi	822	♂	S2	FP	S1	5	4	1
8.vi	31.v	794	♂	P7	F	Q8	7	10	8
8.vi	6.vi	476	♂	R6	R	R8	10	11	2
20.vi	6.vi	819	♂	P6	F	S7	16	20	14
20.vi	6.vi	748	♂	S6	R	S7	5	6	4
21.vi	20.vi	872	♂	P1	FP	Q1	-	1	1
23.vi	6.vi	774	♂	S8	RO	P6	18	22	*
25.vi	21.vi	878	♀	S8	FP	T8	5	8	*

Appendix 6.9: (Continued)

(iii) (continued)

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
26.vi	21.vi	722	♂	X4	OF	V5	11	7	5
26.vi	6.vi	824	♂	T1	P	X3	18	21	20
28.vi	21.vi	880	♂	W2	P	V8	31	34	*
29.vi	6.vi	823	♂	S8	RO	Q5	18	22	23

(iv) Beetles released at 8m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.v	9.v	600	♂	Q6	OF	R6	5	12	7
29.v	9.v	733	♂	V3	FP	Q3	15	15	20
31.v	9.v	734	♀	W1	F	S1	15	7	22
2.vi	1.vi	8	♀	V8	R	X8	10	2	1
5.vi	9.v	732	♀	V3	FP	V4	5	12	27
8.vi	7.vi	796	♀	R8	P	R7	5	3	1
8.vi	7.vi	827	♂	W3	FP	V2	7	1	1
8.vi	7.vi	828	♂	X5	P	X6	5	13	1
9.vi	1.vi	722	♂	S2	OF	X6	28	30	8
10.vi	1.vi	752	♂	R2	PR	V3	16	14	9
12.vi	7.vi	822	♂	S1	P	Q1	10	13	5
13.vi	7.vi	716	♀	V1	R	V6	25	26	6
14.vi	7.vi	826	♀	V2	OF	T4	11	3	7
19.vi	7.vi	829	♂	X7	OF	T4	21	23	*
25.vi	23.vi	887	♂	X4	F	S2	22	16	*
26.vi	23.vi	657	♂	X4	F	T5	16	9	3
28.vi	7.vi	757	♂	P7	PR	P7	-	8	*
28.vi	23.vi	884	♀	T6	O	R7	11	10	*
29.vi	23.vi	791	♂	W1	O	R2	21	20	6
29.vi	23.vi	849	♂	T3	F	R2	11	5	6
29.vi	23.vi	776	♂	S4	P	R3	7	6	6

(v) Beetles released at 12m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
24.v	22.v	713	♂	T7	FP	V5	11	14	2
29.v	22.v	754	♂	R8	P	X5	29	25	7
2.vi	22.v	756	♂	S8	FP	Q6	14	2	11
2.vi	22.v	777	♂	T3	P	S2	7	9	11
4.vi	2.vi	785	♂	P6	O	P6	-	12	*
7.vi	22.v	757	♂	V7	OF	P7	25	19	16
9.vi	8.vi	358	♂	X4	P	X4	-	12	1
10.vi	8.vi	788	♂	S3	RO	T6	16	7	2
16.vi	2.vi	756	♂	Q6	R	R6	5	7	14
16.vi	8.vi	827	♂	V2	F	S2	10	2	8

Appendix 6.9: (Continued)

(v) (continued)

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.vi	8.vi	835	♂	V6	PR	X6	10	8	8
19.vi	8.vi	497	♂	R1	O	R2	5	7	*
20.vi	8.vi	828	♂	X6	F	P2	40	30	12
21.vi	2.vi	8	♀	X8	FP	T7	15	8	19
28.vi	25.vi	889	♂	Q1	R	V2	21	9	*

(vi) Beetles released at 15m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
24.v	21.v	745	♂	V8	F	R7	16	5	3
24.v	5.v	722	♂	S1	P	X4	21	36	19
26.v	21.v	738	♂	P5	O	T8	25	20	3
30.v	23.v	766	♀	W7	R	V8	7	21	7
1.vi	21.v	752	♂	W6	P	R2	28	21	11
1.vi	5.v	721	♂	S1	P	S4	15	30	27
4.vi	23.v	759	♂	P4	F	S3	16	30	*
4.vi	23.v	763	♀	R8	PR	S6	11	6	*
6.vi	21.v	748	♂	S3	O	S6	15	1	16
13.vi	9.vi	208	♂	Q5	R	V4	21	7	4
17.vi	9.vi	842	♂	X4	PR	X5	5	16	8
19.vi	9.vi	838	♂	P2	FP	R1	11	22	*
20.vi	23.v	765	♀	S8	P	V5	18	10	28
21.vi	9.vi	722	♂	X6	FP	X4	10	11	12
26.vi	9.vi	839	♂	T3	PR	X7	25	31	17
29.vi	9.vi	778	♀	R7	FP	Q6	7	8	20
26.vii	28.vi	788	♂	X2	P	V3	11	22	28

(vii) Beetles released at 20m

DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
16.vi	10.vi	608	♂	W2	O	T6	22	10	6
20.vi	10.vi	788	♂	T6	PR	X1	29	11	10
23.vi	10.vi	849	♂	T3	R	T3	-	20	*
23.vi	10.vi	846	♀	P8	PR	V8	25	18	*

Appendix 6.10: Recapture records for Pterostichus niger adults:PX18 Grid, 1978

(Abbreviations as per Appendix 6.2)

	DRC	DRL	IM	Sex	SRL	DD	SRC	d(t)	d(b)	t
Beetles released at 1m	: none recaptured									
Beetles released at 2m	6.v	5.v	302	♀	W2	PR	W1	5	3	1
Beetles released at 4m	: none recaptured									
Beetles released at 8m	28.vi	23.vi	310	♀	T8	P	W3	27	20	*
Beetles released at 12m	: none recaptured									
Beetles released at 15m	: none recaptured									
Beetles released at 20m	: none recaptured									

Appendix 6.11: Comparison of recapture rates following experimental displacement

Basic formula (Brandt and Snedecor's formula)
following Bailey (1964):

$$\chi^2 = \frac{\sum \frac{a^2}{n} - \frac{A^2}{N}}{k(1-k)}$$

.....a.....	A
.....b.....	B
.....n.....	N

General contingency table with 2 rows

where 'k' = A/N, and '1-k' = B/N

Nebria brevicollis ♂♂ Sept/Oct 1977 (Table 6.1i)

Displacement of release (m)	1	2	4	8	12	15	Total
Number recaptured (30 days)	8	19	44	20	15	43	149
(difference)	5	16	34	20	23	38	136
Released	13	35	78	40	38	81	285

$\chi^2 = 3.639$

5 degrees of freedom
0.70 > P > 0.50
No significant difference

Nebria brevicollis ♀♀ Sept/Oct 1977 (Table 6.1i)

Displacement of release (m)	(1 / 2)	4	8	12	15	Total
Number recaptured (30 days)	(- 14)	13	4	7	10	48
difference	(2 + 8)	19	12	8	23	72
Released	(2 +22)	32	16	15	33	120

$\chi^2 = 6.437$

4 degrees of freedom
0.20 > P > 0.10
No significant difference

Appendix 6.11: (Continued)

Pterostichus madidus ♂♂ May/Nov 1977 (Table 6.1ii)

Displacement of release (m)	1	(2 / 4)	(8 / 12 / 15)	Total	
Number recaptured (30 days)	5	(6 -)	(1 + 1 + 6)	19	$\chi^2 = 0.0326$ 2 degrees of freedom 0.99>P>0.98 No significant difference
difference	105	(78 +40)	(43+ 66 + 42)	374	
Released	110	(84 +40)	(44+ 67 + 48)	393	

Pterostichus madidus ♀♀ May/Nov 1977 (Table 6.1ii)

Displacement of release (m)	1	(2 / 4)	(8 / 12 / 15)	Total	
Number recaptured (30 days)	15	(3 + 2)	(1 + 4 + 1)	26	$\chi^2 = 6.414$ 2 degrees of freedom 0.05>P>0.02 ∴ Significant difference
difference	142	(63 + 67)	(59 + 41 + 54)	426	
Total released	157	(66 + 69)	(60 + 45 + 55)	452	

Pterostichus madidus ♂♂ Apr/June 1978 (Table 6.2iii)

Displacement of release (m)	1	2	4	8	12	(15/20)	Total	
Number recaptured	13	5	5	4	4	(4 + 2)	37	$\chi^2 = 0.468$ 5 degrees of freedom p>0.99 No significant difference
Not recaptured	50	17	15	19	15	(21+ 4)	141	
Total Released	63	22	20	23	19	(25 +6)	178	

P. madidus ♀♀ Apr/June 1978 (Table 6.2iii)

Displacement of release (m)	1	2	4	(8 / 12)	(15/20)	Total	
Recaptures	24	11	13	(5 + 2)	(7 + 2)	64	$\chi^2 = 8.546$ 4 degrees of freedom 0.10>P>0.05 No significant difference
non recaptures	122	54	42	(36 + 52)	(43+23)	372	
Total Released	146	65	55	(41 + 54)	(50+25)	436	

Appendix 6.11 (Continued)

Abax parallelepipedus ♂♂ Apr/June 1978 (Table 6.2iv)

Displacement of release (m)	1	2	4	8	12	(15/20)	Total
Recaptures	26	23	13	14	14	(13+ 3)	106
Non recaptures	34	24	9	18	28	(22+ 3)	138
Total released	60	47	22	32	42	(35+ 6)	244

$\chi^2 = 4.844$

5 degrees of freedom
 $0.50 > P > 0.30$
 No significant difference

Abax parallelepipedus ♀♀ Apr/June 1978 (Table 6.2iv)

Displacement of release (m)	1	(2 / 4)	(8 / 12)	(15 / 20)	Total
Recaptures	8	(7 + 3)	(7 + 1)	(4 + 1)	31
Non recaptures	21	(9 + 9)	(6 + 11)	(11 + 4)	71
Total released	29	(16+12)	(13+12)	(15 + 5)	102

$\chi^2 = 0.788$

3 degrees of freedom
 $0.90 > P > 0.80$
 No significant difference

Pterostichus niger ♂♂ 1977 (Table 6.1v)

Displacement of release (m)	(1 / 2)	4	8	(12 / 15)	Total
Recaptures	(- 10)	4	9	(7 + 2)	32
Non recaptures	(14+16)	15	10	(40+ 9)	104
Total released	(14+26)	19	19	(47+11)	136

$\chi^2 = 7.361$

3 degrees of freedom
 $0.10 > P > 0.05$
 No significant difference

P. niger ♀♀ 1977 (Table 6.1v)

Displacement of release (m)	(1 / 2)	(4 / 8)	(12 / 15)	Total
Recaptures	(2 + 4)	(8 + 3)	(10 + 1)	28
Non recaptures	(16+18)	(15+22)	(42 + 19)	132
Total released	(18+22)	(23+25)	(52 + 20)	160

$\chi^2 = 1.395$

2 degrees of freedom
 $P \approx 0.50$
 No significant difference

N.B. Where figures fall below 4 or 5 they are combined to an adjacent category in order to avoid errors due to small sample size.

Appendix 7.1: Individual capture histories of *Nebria brevicollis* beetles : multiple recaptures

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) Bracketed figures refer to release day, where different to capture day.
198	13(16).ii. 1976 E4 1m 8.x. 1976 F4 1m OF 29.ix. 1976 E4 1m OF 25.x. 1976 D4 1m P 30.ix. 1976 F3 1m P 18.xi. 1976 C4 1m P
233 ♂	24.ii. 1976 G6 1m 26(27).x. 1976 E6 1m FP 1.x. 1976 D6 1m OF 11.xi. 1976 E7 1m PR 4(5). x. 1976 F7 1m O 2.iii. 1977 C6 1m R
320 ♂	16.iii. 1976 B8 1m 18.x. 1976 A7 1m PR 10.x. 1977 G5 12m O 14.ix. 1976 A7 1m PR 19(20).x. 1976 A7 1m R 11(12).x. 1976 B10 1m FP 4.x. 1977 G5 2m PR
436 ♀	29.iii. 1976 B7 1m 20.ix. 1976 C7 1m F 8.x. 1976 B10 1m F 12.iv. 1976 C6 1m 27.ix. 1976 A7 1m R0 1.xi. 1976 E6 1m PR 16.ix. 1976 C6 1m F 4(5).x. 1976 C8 1m R0 10.i. 1977 F4 dead
590	14.iv. 1976 A8 1m 13.x. 1976 C4 1m OF 26(29).x. 1976 C4 1m OF 24.ix. 1976 B4 1m R 14.x. 1976 C4 1m F 11(12).x. 1976 C4 1m O 25.x. 1976 D3 1m R0
647 ♂	7.v. 1976 G6 1m 11(12).x. 1976 A3 1m O 10.x. 1977 E3 dead 1.x. 1976 A9 1m R 18.x. 1976 C4 1m P 8.x. 1976 B7 1m OF 19(20).x. 1976 C3 1m F
755	15.ix. 1976 C4 1m P 1.xi. 1976 B6 1m PR 11(12).x. 1976 A7 1m OF 2.xi. 1976 B6 1m R 13.x. 1976 A7 1m FP 17.xi. 1976 A7 1m

Appendix 7.1: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) Bracketed figures refer to release day, where different to capture day.	
798 ♂	17.ix. 1976 A5 1m PR 15.x. 1976 C6 1m O 19.x. 1977 H0 2m PR	4(5).x. 1976 A7 1m P 30.ix. 1977 E9 8m FP 28.x. 1977 H7 12m F
888 ♂	20.ix. 1976 D10 1m P 1.x. 1976 C7 1m RO	24.ix. 1976 D10 1m R 6(7).x. 1976 D6 1m FP
904	21.ix. 1976 A4(A5) 1m PR 11(12).x. 1976 E3 1m OF 19(20).x. 1976 E4 1m R	23.ix. 1976 A4 1m RO 13.x. 1976 E3 1m F
980 ♂	23.ix. 1976 E7 1m FP 26(27).x. 1976 B6 1m FP 26.xi. 1976 C6 1m P	25.ix. 1976 G8 1m RO 29.x. 1976 B6 1m P
1010	24.ix. 1976 C3 1m F 22.x. 1976 C4 1m RO 3.xi. 1976 C4 1m R	4(5).x. 1976 C6 1m O 26(27).x. 1976 C4 1m OF 18.xi. 1976 C4 1m P
1040	24.ix. 1976 E4 1m PR 8.x. 1976 F3 1m OF 15.x. 1976 G4 1m OF	27.ix. 1976 E4 1m RO 11(12).x. 1976 F4 1m F
1048 ♂	24.ix. 1976 E4 1m PR 13.x. 1976 C6 1m R	25.ix. 1976 E4 1m R 14.x. 1976 C6 1m RO
1094	28(29).ix. 1976 B6 1m P 7.x. 1976 D3 1m RO	30.ix. 1976 B6 1m R 8.x. 1976 D3 1m O
1143 ♂	28.ix. 1976 F4 1m FP 28.x. 1976 B7 1m FP	4(5).x. 1976 G7 1m F 19.x.1977 C7 2m PR
		14.x. 1976 C6 1m RO 17.x. 1977 F8 1m FP 8. xi. 1977 E7 1m P
		27.ix. 1976 D8 1m P 11.x. 1976 D6 1m P
		29.ix. 1976 D4 1m RO 18.x. 1976 E4 1m PR
		25.x. 1976 B6 1m F 1.xi. 1976 B6 1m PR
		11(12).x. 1976 C6 1m P 2.xi. 1976 C4 1m PR
		4(5).x. 1976 F3 1m R 13.x. 1976 E4 1m FP
		5.x. 1976 E4 1m PR 25.x. 1976 A5 1m
		4(5).x. 1976 D3 1m R 13.x. 1976 G2 1m O
		18(19).x. 1976 B6 1m OF 20.x. 1977 C7 15m R

Appendix 7.1: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) Bracketed figures refer to release day, where different to capture day.
1223	29.ix. 1976 F3 1m FP 11(12).x. 1976 G2 1m RO 1.x. 1976 F3 1m PR 22.x. 1976 G2 1m F 4(5).x. 1976 G4 1m F 25.x. 1976 G2 1m FP
1235	29.ix. 1976 F10 1m FP 21(23).x. 1977 E9 1m RO 4.i. 1978 E5 25.x. 1976 F3 1m O 31.x. 1977 C7 4m FP 26.x. 1976 F3 1m OF 29.xii. 1977 E5 4m F
1298	1.x. 1976 A7 1m FP 4.iii. 1977 A7 1m RO 8.xi. 1976 A5 1m RO 7.x. 1977 A7 4m PR 8.ii. 1977 A7 1m R 10.x. 1977 P4 1m F
1379	4(5).x. 1976 D4 1m F 26(27).x. 1976 C4 1m OF 11(12).x. 1976 C4 1m O 22.xi. 1976 C4 1m PR 13.x. 1976 C4 1m OF 8.xii. 1976 C4 1m
1422	4(5).x. 1976 E7 1m O 27.x. 1976 F8 1m PR 26.x. 1977 G5 15m O 6(7).x. 1976 E8 1m O 27.ix. 1977 F7 15m PR 27(28).x. 1977 F8 1m O 11(12).x. 1976 E6 1m F 21(23).x. 1977 E9 1m RO
1423	4(5).x. 1976 E7 1m O 11((12).x. 1976 C6 1m P 29.x. 1976 C7 1m F 7.x. 1976 C7 1m R 26(27).x. 1976 C7 1m O 8.x. 1976 C7 1m RO 28.x. 1976 C7 1m OF
1454	4(5).x. 1976 G7 1m F 25.x. 1976 D7 1m RO 6(7).x. 1976 F7 1m OF 1.xi. 1976 C6 1m F 11(12).x. 1976 E7 1m FP 12.xi. 1976 C6 1m
1467	4(5).x. 1976 G10 1m RO 28.x. 1976 C4 1m F 19(20).x. 1976 C6 1m F 1.xi. 1976 C4 1m P 26(27).x. 1976 C4 1m OF 2.xi. 1976 C4 1m
1524	6(7).x. 1976 F6 1m OF 26(27).x. 1976 E7 1m O 22.xi. 1976 C7 1m P 8.x. 1976 F6 1m FP 8.xi. 1976 C6 1m PR 23.xi. 1976 C7 1m PR 11(12).x. 1976 E6 1m F 17.xi. 1976 C6 1m O

Appendix 7.1 (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)	
	Bracketed figures refer to release day, where different to capture day.	
1544 ♂	7.x. 1976 C7 1m R 26(27).x. 1976 A8 1m F	15.x. 1976 A7 1m P 8.xii. 1976 C6 1m R 25.x. 1976 A8 1m OF 8.ii. 1977 C6 1m
1790 ♂	15.x. 1976 C3 1m OF 22.x. 1976 E11 1m PR	20.x. 1976 E4 1m RO 28.ix. 1977 A11 1m R 21.x. 1976 E2 1m R 11.v. 1977 A12
1806 ♂	15.x. 1976 F7 1m RO 12.x. 1977 N4 1m R	7.x. 1977 M3 1m O 19.x. 1977 N4 1m OF 10.x. 1977 M3 1m OF 15.iii. 1978 L5 1m
1828 ♂	18.x. 1976 C6 1m OF 17.x. 1977 B9 1m O 11.xi. 1977 N4 1m	5.xi. 1976 A9 1m P 20.x. 1977 L1 1m RO 12.x. 1977 B9 1m PR 8.xi. 1977 N4 1m FP
1946	28.x. 1976 C4 1m F 19.xi. 1976 G6 1m O 7.xii. 1976 E6 1m	1.xi. 1976 E4 1m RO 29.xi. 1976 E6 1m R .2.xi. 1976 F3 1m FP 30(1).xi. 1976 E6 1m RO
1/465 ♂	22.ix. 1977 B3 1m O 21(23).x. 1977 G5 1m R	13.x. 1977 B3 1m F 2.xi. 1977 H3 12m OF 14.x. 1977 C3 2m R 4.xi. 1977 H4
1/480 ♂	23.ix. 1977 E3 12m P 6.x. 1977 E4 15m P	4.x. 1977 E4 2m F 10.x. 1977 E3 12m P 5.x. 1977 E4 8m FP 24.x. 1977 E3
1/493 ♂	23.ix. 1977 A12 12m R 14.x. 1977 A12 2m O	2.x. 1977 A12 12m F 17.x. 1977 A12 1m OF 7.x. 1977 A12 4m PR 21.x. 1977 A12
1/561 ♀	26.ix. 1977 M5 1m R 30.ix. 1977 M4 1m RO 14.x. 1977 M3 1m F	27.ix. 1977 N3 1m O 2.x. 1977 M4 1m O 19.x. 1977 N4 1m OF 29.ix. 1977 M4 1m R 4.x. 1977 N4 1m FP 20.x. 1977 N4 1m

Appendix 7.1: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) Bracketed figures refer to release day, where different to capture day.	
1/564 ♂	26.ix. 1977 N4 1m PR 30.ix. 1977 N4 1m OF 12.x. 1977 P1 1m O 3.xi. 1977 C4 12m F	27.ix. 1977 N4 1m R 2.x. 1977 N4 1m F 19.x. 1977 P4 1m PR 3.iv. 1978 B7 29.ix. 1977 N4 1m O 4.x. 1977 N4 1m FP 2.xi. 1977 C4 12m OF
1/609 ♂	28.ix. 1977 A4 4m P 17.x. 1977 C8 1m R 3.xi. 1977 A7	30.ix. 1977 C5 8m FP 24.x. 1977 B9 8m P 14.x. 1977 C8 2m PR 27.x. 1977 B9 1m R
1/629 ♂	28.ix. 1977 F4 4m O 20.x. 1977 E4 15m P 27.iv. 1978 Q5	7.x. 1977 F4 4m P 14.xi. 1977 H7 2m R 17.x. 1977 F4 1m R 13.iii 1978 G6 1m FP
1/706 ♂	2.x. 1977 N4 1m F	4.x. 1977 N4 1m FP 12.x. 1977 N4 1m R 6.x. 1977 N4 1m P 14.x. 1977 N4 1m
1/733 ♂	4.x. 1977 G10 2m O 10.x. 1977 G8 12m O 29.xi. 1977 H7	6.x. 1977 H9 15m OF 24.x. 1977 H6 8m P 7.x. 1977 F8 4m R 14.xi. 1977 H7 2m R
1/751 ♂	5.x. 1977 E1 8m OF 19.x. 1977 E1 2m O	14.x. 1977 E1 2m R 28.x. 1977 E1 12m PR 17.x. 1977 E1 1m R0 14.xi. 1977 G2
1/829 ♂	10.x. 1977 B9 12m P 31.x. 1977 B8 4m FP	17.x. 1977 B9 1m O 29.xi. 1977 A6 1m P 21.x. 1977 B9 1m FP 3.iv. 1978 A6

Appendix 7.2: Individual capture histories of *Nebria brevicollis* beetles : long-lived beetles

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) *Individual capture histories illustrated in 7.210
107 ♂	11.x. 1976 D3 1m OF 22.x. 1976 C2 1m R 23.v. 1977 A11 1m
233 ♂	1.x. 1976 D6 1m OF 4.x. 1976 F7 1m O 11.xi. 1976 E7 1m PR 2.iii. 1977 C6 1m
278 ♂	21.ix. 1976 F7 1m P 8.x. 1976 E6 1m OF 10.ii. 1977 C6 1m
*320 ♂	14.ix. 1976 A7 1m PR 11.x. 1976 B10 1m FP 19.x. 1976 A7 1m R 4.x. 1977 G5 2m PR
*436 ♀	12.iv. 1976 C6 1m 16.ix. 1976 C6 1m F 27.ix. 1976 A7 1m RO 4.x. 1976 C8 1m RO 8.x. 1976 B10 1m F 10.i. 1977 F4 1m
465 ♂	11.xi. 1976 G5 1m O 22.xi. 1976 F3 1m OF
558 ♂	4.x. 1976 C6 1m O 25.x. 1976 F8 1m P
588 ♂	22.xi 1976 E3 1m FP 12.x. 1977 E1 8m
602 ♂	2.iii. 1977 F11 1m
*647 ♂	7.v. 1976 G6 1m 8.x. 1976 B7 1m OF 11.x. 1976 A3 1m O 19.x. 1976 C3 1m F 10.x. 1977 E3 12m

Appendix 7.2: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6) *Individual capture histories illustrated in 7.210	
769	♂	15.ix. 1976 G5 1m P 8.xi. 1977 F7 1m F 24.ii. 1978 E6 15m
1125	♂	28.ix. 1976 D8 1m PR 6.x. 1978 V6 12m 6.x. 1976 F8 1m FP 24.x. 1977 H7 8m O
*1235	♀	29.ix. 1976 F10 1m FP 25.x. 1976 F3 1m O 26.x. 1976 F3 1m OF 21.x. 1977 E9 1m RO 31.x. 1977 C7 4m FP 29.xii. 1977 E5 4m F 4.i. 1978 E5 15m
1416	♂	4.x. 1976 E4 1m P 4.iii. 1977 E4 1m O 30.iv 1978 Q2 1m
1805	♂	15.x. 1976 F4 1m PR 8.xi. 1976 F3 1m PR 3.v 1978 S2 2m
1806	♂	15.x. 1976 F7 1m RO 7.x. 1977 M3 1m O 10.x. 1977 M3 1m OF 12.x. 1977 N4 1m R 19.x. 1977 N4 1m OF 15.iii. 1978 L5 1m
1841	♂	18.x. 1976 F7 1m O 28.iii. 1978 F4 1m
1942	♂	27.x. 1976 G7 1m P 28.iv. 1978 S2 1m
1/239	♂	1.xii. 1976 E1 1m FP 29.xii. 1976 E1 1m R 24.ii. 1978 H6 15m
1/269	♂	3.iii. 1977 B8 1m RO 29.xi. 1977 C4 1m R 23.ii. 1978 H7 12m

Appendix 7.3: Individual capture histories of Pterostichus madidus beetles : multiple recaptures

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6). Bracketed figures refer to release day, where different to capture day.
63 ♂	1.iii. 1976 A5 1m 12.iv. 1976 A5 1m 17.iii. 1976 A5 1m 25.iii 1976 A5 1m
105 ♂	25.iii. 1976 B8 1m 30.viii. 1976 B6 1m 26.iii 1976 B8 1m 2.viii. 1976 E6 1m FP
162 ♀	1.iv. 1976 C6 1m 26.v. 1976 D7 1m 2.iv. 1976 C6 1m 12.iv. 1976 C6 1m
2/688 ♂	29.vi. 1977 D10 1m O 22.viii. 1977 D6 12m 7.viii. 1977 E8 1m OF 11.viii. 1977 E7 15m OF
2/747 ♂	19.vii. 1977 D8 1m FP 28.vi. 1978 V6 15m 10.vi. 1978 P2 20m P 21.vi. 1978 I1 4m OF
2/807 ♂	2.viii. 1977 E5 8m F 20.iii. 1978 L1 1m 9.xi. 1977 L1 1m O 10.xi. 1977 L1 1m OF
3/401 ♂	13.ix. 1977 N5 1m F 20.x. 1977 N2 1m 16.ix. 1977 M4 1m P 12.x. 1977 N2 1m OF
3/643 ♂	19.iv. 1978 G6 8m R 23.vi. 1978 P1 8m 9.v. 1978 V3 8m FP 11.vi. 1978 W4 12m OF
3/692 ♀	1.v. 1978 Q2 20m R 29.v. 1978 S2 1m RO 8.v. 1978 V1(V2) 12m OF 17.vi. 1978 Q2 1m 28.v. 1978 R1 1m P
3/798 ♂	9.v. 1978 W4 8m R 20.vi. 1978 S3(I3) 4m FP 31.vx. 1978 X4 4m RO 29.vi. 1978 W3 1m 9.vi 1978 W2 15m RO

Appendix 7.3: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6). Bracketed figures refer to release day, where different to capture day.	
3/807 ♀	10.v. 1978 R2 2m OF 11.vi. 1978 P1 12m	16.v. 1978 T3 2m F 31.v. 1978 P3 4m R
4/529 ♂	12.vi. 1978 V5 2m FP 26.vi. 1978 R1 15m	23.vi. 1978 V4 8m FP 25.vi. 1978 T3 12m FP

Appendix 7.4: Individual capture histories of Pterostichus madidus beetles : long-lived individuals

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)	
118	♂	26.iii. 1976 G5 1m
176	♀	2.iv. 1976 D7 1m
230	♀	12.iv. 1976 A2 1m
327	♂	5.v. 1976 C6 1m
422	♀	7.v. 1976 C5 1m
433	♀	7.v. 1976 D10 1m
499	♀	10.v. 1976 F6 1m
623	♂	24.v. 1976 D6 1m O
628	♀	24.v. 1976 E6 1m FP
697	♀	28.v. 1976 F7 1m PR
742	♀	1.vi. 1976 E1 1m R
765	♀	2.vi. 1976 D1 1m PR
815	♀	4.vi. 1976 F1 1m PR
855	♀	7.vi. 1976 D9 1m R0
1063	♀	14.vi. 1976 G5 1m OF
1/22	♂	16.vi. 1976 F6 1m PF
1/62	♀	17.vi. 1976 G9 1m OF
1/85	♀	18.vi. 1976 F10 1m F
1/135	♂	22.vi. 1976 B2 1m OF
1/145	♂	22.vi. 1976 D6 1m R
1/176	♀	2.vii. 1976 E9 1m O
1/233	♀	20.vii. 1976 C11 1m
1/265	♀	23.vii. 1976 F6 1m P
1/356	♂	28.vii. 1976 C3 1m R
1/365	♀	28.vii. 1976 E6 1m PR
1/378	♂	29.vii. 1976 D3 1m O
1/409	♂	2.viii. 1976 A9 1m O
1/422	♂	2.viii. 1976 D4 1m F
1/738	♂	25.viii. 1976 C8 1m P
1/982	♀	18.iii. 1977 G5 1m FP
		26.iii. 1976 G5 1m
		2.iv. 1976 D7 1m
		12.iv. 1976 A2 1m
		5.v. 1976 C6 1m
		7.v. 1976 C5 1m
		7.v. 1976 D10 1m
		10.v. 1976 F6 1m
		24.v. 1976 D6 1m O
		24.v. 1976 E6 1m FP
		28.v. 1976 F7 1m PR
		1.vi. 1976 E1 1m R
		2.vi. 1976 D1 1m PR
		4.vi. 1976 F1 1m PR
		7.vi. 1976 D9 1m R0
		14.vi. 1976 G5 1m OF
		16.vi. 1976 F6 1m PF
		17.vi. 1976 G9 1m OF
		18.vi. 1976 F10 1m F
		22.vi. 1976 B2 1m OF
		22.vi. 1976 D6 1m R
		2.vii. 1976 E9 1m O
		20.vii. 1976 C11 1m
		23.vii. 1976 F6 1m P
		28.vii. 1976 C3 1m R
		28.vii. 1976 E6 1m PR
		29.vii. 1976 D3 1m O
		2.viii. 1976 A9 1m O
		2.viii. 1976 D4 1m F
		25.viii. 1976 C8 1m P
		18.iii. 1977 G5 1m FP
		4.iii. 1977 F5 1m
		13.v. 1977 F6 2m
		5.v. 1977 B3 1m
		2.viii. 1978 Q4 1m
		16.ix. 1977 L5 12m
		10.v. 1976 D10 1m
		11.v. 1976 F6 1m
		28.v. 1978 V3 1m
		28.vi. 1978 W3 1m
		23.v. 1978 T4 15m R0
		17.x. 1977 F2 1m P
		17.x. 1977 F2 1m
		3.vi. 1977 F2 1m
		17.x. 1977 D8 1m
		9.v. 1978 T1 8m
		23.vi. 1977 E6 2m
		16.v. 1978 W7 2m
		23.v. 1978 R3 15m
		23.v. 1977 D2 8m
		15.viii. 1977 D8 2m
		23.v. 1978 S8 15m
		2.viii. 1976 C11 1m
		24.v. 1978 S1 2m
		16.viii. 1977 C2 12m
		19.x. 1977 F7 2m
		6.viii. 1977 A9 1m
		24.vi. 1977 B9 15m
		7.iii. 1977 E3 1m O
		26.iv 1978 T4 15m F
		4.i. 1978 F4 15m
		3.viii. 1978 Q4 1m
		2.v. 1977 D10 1m
		11.xi. 1977 D8 15m
		30.v. 1978 V6 2m
		24.x. 1977 F2 8m
		30.v. 1977 C1 1m
		29.vi. 1977 E5 1m
		8.v. 1978 Q4 1m

Appendix 7.4: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)	
2/321	♀	2.v. 1977 G8 1m FP
2/444	♀	23.v. 1977 F3 8m P
2/486	♀	26.v. 1977 G7 1m R
2/664	♂	26.vi. 1977 E4 1m FP
2/686	♂	29.vi. 1977 D7 1m FP
2/697	♂	29.vi. 1977 F9 1m F
2/712	♀	30.vi. 1977 C7 2m O
2/719	♀	30.vi. 1977 F6 2m PR
2/747	♂	19.viii. 1977 D8 1m FP
		28.vi. 1978 V6 15m
2/750	♂	19.viii. 1977 E10 1m P
2/785	♂	25.viii. 1977 H4 15m P
2/789	♀	26.viii. 1977 H6 4m R0
		1.v. 1978 W6 20m
		6.vi. 1978 Q1 4m
		1.v. 1978 X8 20m
		25.vi. 1978 W4 12m
		29.vi. 1978 S3 1m
		19.vi. 1978 Q6 1m
		24.v. 1978 R1 2m FP
		1.v. 1978 T3 20m
		10.vi. 1978 P2 20m P
		11.v. 1978 Q3 4m
		15.vi. 1978 T7 1m
		8.vi. 1978 T2 12m
		9.vi. 1978 R4 15m
		21.vi. 1978 T1 4m OF

Appendix 7.5: Individual capture histories of Abax parallepipedus beetles : multiple recaptures

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)
8 ♀	12.iv. 1976 G6 1m 21.vi. 1978 T7 4m 1.vi. 1978 V3 8m R 2.vi. 1978 X8 12m FP
71 ♂	10.v. 1976 C4 1m 4.viii. 1976 B4 1m 27.vii. 1976 B4 1m PF 28.vii. 1976 B4 1m P
208 ♂	8.vi. 1976 B10 1m P 9.vi. 1978 Q5 15m R 14.vi. 1977 A2 2m R0 13.vi. 1978 V4 1m 5.vi. 1978 V6 2m P
476 ♂	9.v. 1977 D8 1m F 8.vi. 1978 R8 12m 27.v. 1977 F7 1m P 6.vi. 1978 R6 4m R
608 ♂	1.viii. 1977 G7 1m FP 17.vi. 1978 Q5 1m 10.vi. 1978 W2 20m O 16.vi. 1978 T6 1m R
657 ♂	15.viii. 1977 G7 2m O 26.vi. 1978 T5 15m 16.v. 1978 W7 2m PR 23.vi. 1978 X4 8m F
684 ♀	25.viii. 1977 G6 12m O 12.vi. 1978 T1 2m 2.v. 1978 T4 2m P 30.v. 1978 R1 2m PR
716 ♀	4.v. 1978 W1 4m OF 13.vi. 1978 V6 1m O 29.v. 1978 X4 1m PR 26.vi. 1978 T5 15m 7.vi. 1978 V1 8m R
722 ♂	5.v. 1978 S1 15m P 9.vi. 1978 X6 15m FP 24.v. 1978 X4 2m FP 21.vi. 1978 X4 4m OF 1.vi. 1978 S2 8m OF 26.vi. 1978 V5 15m

Appendix 7.5: (Continued)

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)		
730 ♀	8.v. 1978 T7 1m OF 1.vi. 1978 S7 8m	24.v. 1978 V8 2m FP	30.v. 1978 T6 2m OF
745 ♂	16.v. 1978 W6 2m FP 8.vi. 1978 S8 12m	21.v. 1978 V8 15m F	24.v. 1978 R7 2m F
756 ♂	22.v. 1978 S8 12m FP 3.viii. 1978 Q7 1m	2.vi. 1978 Q6 12m R	16.vi. 1978 R6 1m F
759 ♂	23.v. 1978 P4 15m F 29.vi. 1978 T1 1m	4.vi. 1978 S3 1m R	14.vi. 1978 P2 1m R0
776 ♂	28.v. 1978 SE 1m FP 16.vi. 1978 Q1 1m OF	29.v. 1978 V1 1m P 26.vi. 1978 S4 8m P	4.vi. 1978 R2(R3) 1m R0 29.vi. 1978 R3 1m
785 ♂	30.v. 1978 P7 2m OF 23.vi. 1978 Q4 8m	2.vi 1978 P6 12m O	4.vi. 1978 P6 1m OF
788 ♂	30.v. 1978 S2 2m O 20.vi. 1978 X1 2m F	8.vi. 1978 S3 12m R0 28.vi. 1978 X2 15m P	10.vi. 1978 T6 20m PR 26.vii. 1978 V3 1m
790 ♂	30.v. 1978 V8 2m PR 23.vi. 1978 R8 8m	4.vi. 1978 T6 1m FP	5.vi. 1978 T7 2m PR

Appendix 7.6: Individual capture histories of *Abax parallelepipedus*: long-lived beetles

Individual code number and sex	Dates of successive captures, locations and release points (see Chapters 2 and 6)			
	*overwintered beetles	**this beetle soft, and obviously callow on 18.x. 1976		
*8	♀	12.iv. 1976 G6 1m 21.vi. 1978 T7 4m 14.iv. 1976 E4 1m 10.v. 1976 D5 1m 11.v. 1976 G7 1m 24.v. 1976 F8 1m F 8.vi. 1976 B10 1m P 9.vi. 1978 Q5 15m R 14.vi. 1976 C8 1m P 17.vi. 1976 F5 1m O 21.vi. 1976 F5 1m OF 29.vi. 1976 B6 1m F 1.vii. 1976 F5 1m FP 18.x. 1976 G7 1m OF	1.vi. 1978 V8 8m R 13.vi. 1977 B6 2m 17.viii. 1977 F7 12m P 21.vi. 1978 V1 4m 11.v. 1978 P6 4m PR 14.vi. 1977 A2 2m R0 13.vi. 1978 V4 1m 15.vi. 1976 C8 1m PR 6.v. 1978 Q4 12m 13.vi. 1978 Q1 1m R0 9.vi. 1978 V1 15m 8.vi. 1978 X4 12m P 2.v. 1978 S6 2m PR	2.vi. 1978 X8 12m FP 23.v. 1978 R7 15m 13.vi. 1978 T7 1m 5.vi. 1978 V6 2m P 29.v. 1978 R3 1m 19.vi. 1978 T1 1m 9.vi. 1978 X4 15m 26.vii. 1978 W4 1m
*13	♀			
63	♂			
87	♂			
131	♀			
208	♂			
233	♀			
268	♂			
287	♂			
340	♂			
358	♂			
**462	♀			