STUDIES IN THE ECOLOGY OF CARABIDAE (COLEOPTERA).

by

P.J.M. Greenslade, B.A., D.I.C.

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Sunninghill,
Ascot, Berkshire.

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ABSTRACT.

Aspects of the ecology of Carabidae (Coleoptera) were studied on the Imperial College Field Station from autumn 1958 to autumn 1960.

Sampling was carried out by pitfall traps and it was found that this method did not give a reliable indication of the relative numbers of species. Allowance was made for this during the course of the work.

The life histories of 25 species, common on the Field Station, were investigated with especial reference to annual cycles of adult activity. The vegetation of the drier parts of the Field Station was described and the distribution of the Carabid species related to it. Their daily cycles of activity were investigated and are discussed in relation to habitat and life-history.

Work was carried out on distribution of populations of Nebria brevicollis F. and Pterostichus madidus F. Population densities and dispersal were studied by marking and recapture, and some observations were made on populations of four other species. Boundary and area patterns were described, and distribution and dispersal are discussed in relation to the probable effect of weather as a mortality factor.

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A. INTRODUCTION AND SAMPLING METHODS.

I. INTRODUCTION.

The object of the work described in this thesis was to investigate the distribution of individuals in populations of selected species of Carabidae. It may be placed in context by a brief discussion of the nature of a population.

A population has been defined by Friederichs, quoted by Carpenter (1956), as the sum total of individuals of a species in a given area, while Richards (1960) has suggested as a possible definition that a population is a number of individuals of one species whose lives are sufficiently integrated to have an influence on one another; such a population will normally occupy a spatially fairly well defined area even though the distribution is hardly ever strictly continuous.

The term population therefore carries two meanings, one identifying the total number of individuals in a taxonomic group in an arbitrary area, the other referring to a taxonomically related, but more or less spatially isolated group of individuals, communicating more among themselves than with other such groups of the same taxon. However, the proper use of the term is the first (Shorter Oxford English Dictionary, 1952: 'Population..... the degree in which a place is populated or inhabited; hence, the total number of its inhabitants'), and Gilmour and Gregor (1939) have suggested a terminology to occupy the second meaning. In this a 'deme' is defined as any assemblage of taxonomically closely related individuals, while population in this sense becomes synonymous with 'gamodeme': a deme forming a more or less isolated, local interbreeding community.

The concept of the deme has gained wide acceptance in experimental plant taxonomy, and has been used among zoologists by Carter (1951) and others in discussing evolution at the sub-specific level; however, the term deme has frequently been used for what is strictly an isolated interbreeding population or gamodeme. Here population is used loosely to include both its meanings, as to take any other course would be to anticipate final conclusions.

Although the population is the unit on which much recent ecological discussion has been based, there have been few studies on the spatial structure of populations of terrestrial invertebrates, that is on the pattern of distribution of individuals and on the amount of movement they show.

Such work as has been carried out includes that of Salt and Hollick (1946) and Guild (1952), on the distribution of soil invertebrates, and of Brian (1947, 1952) on patterns of density and movement in adult Elateridae, and on the distribution of nests of certain ant species. MacLeod and Donnelly (1958) and Dowdeswell, Fisher and Ford (1949) have studied movement and dispersal in flying insects. This and other work has established that populations commonly show a non-random distribution which may or may not be attributable to properties of the habitat, and that there is considerable variation in the extent to which spatial changes in vegetation and other natural barriers impede dispersal. However, there remain few cases where any attempt has been made to describe the limits of populations of terrestrial invertebrates, or to establish the presence of gamodemes in a continuous habitat (as opposed to a discontinuous to be found for example

in ponds or on small islands).

Andrewartha and Birch (1954) have argued that distribution and abundance are two aspects of the same phenomenon, and it is difficult to dissociate the problem of the distribution of a population, from that of variation within it in the density of its constituent individuals. Elton (1949) has distinguished populations with area patterns, that is those forming the typical gamodeme, and those with boundary patterns. However he also describes populations with a periodic distribution centred for example on individuals of a plant dominant, and those with an inverse periodic distribution, where an animal may perhaps only occur where the dominant plant does not. A population showing a typical boundary or area pattern may be composed of high density nodes or centres, of either periodic or inverse periodic distribution. It is one purpose of this work to discover the extent to which Carabid populations agree with these, or any other, hypothetical patterns.

A further reason for investigating distribution within populations lies in the context of the factors controlling numbers. Good (1953) has suggested that on the geographical scale plant distribution is limited by climatic factors, while competition and properties of the soil determine abundance within the range of a species. Jeffree (1960) has had some success in relating the distribution of certain insect species to climatic areas, and although Lindroth (1953) has questioned the significance of average properties of the macroclimate, determined over a long period, to insects which are directly affected only by microclimatic factors, the former are evidently important in setting the broad limits of distributions.

Richards (1960) has applied Good's suggestion to insect populations, arguing that at the limit of a specie's range where its distribution is patchy chance effects of climate are important in permitting immigration and causing extinction from place to place. In the centre of the range where the microclimate is optimal a more or less steady state will be maintained by Nicholsonian density-dependent controls, while weather causes only relatively minor fluctuations about this value.

After an investigation on larvae of the Tent Moth Malacosoma pluviale (Dyar), Wellington (1957) has put forward the suggestion that in studying the factors controlling populations seasonal and areal differences in the behaviour, survival ability and physiological responses of individuals must be considered. Similarly Elton (1949) observed that theories about population change and interaction are based on concepts of mean density, and pointed out that populations are in fact split up into groups and centres.

The importance of work on the pattern of distribution in populations becomes apparent with their pleas for greater finesse in studies on these controlling factors, and also if Richards' suggestions on controlling factors are considered in relation to Lindroth's(1953) observations, on the importance of the microclimate. Here the latter stressed that in any large area where the microclimate permits the existence of a species the microclimate will only be suitable in certain parts. This implies the presence of gradients over which physical conditions become increasingly unfavourable. In such zones individuals may be expected to be distributed sparsely and patchily, and living at the limits of their physical tolerance will be especially susceptible to the effects of climatic or other density-independent

factors. In contrast in the physically optimal centre of a population's area, according to Richards' theory density dependent factors will operate. Similar arguments may be applied to an isolated population exploiting only part of a continuously favourable habitat, although in the field it is to be expected that any population, as Elton suggests, is distributed among high density centres, and it is between these, as well as at the periphery, that there may occur local extinction and immigration due to changes in the microclimate.

These considerations are beyond the scope of the experimental work described here, and mortality factors and the physical tolerance of species have not been investigated. However such discussion can only be elaborated and tested after extensive work on the pattern of density in populations and the amount of movement shown by individuals, and it is towards this end that the present work has been directed.

The work done falls into three parts; initially it was necessary to consider methods of sampling and estimating the overall density of populations, and as the methods used depended on the activity of the insects this had to be investigated. Daily and seasonal cycles were considered in conjunction with investigations into aspects of the bionomics of selected species; habitats, life history and daily rhythms of activity were studied. This involved reviewing the literature and relating the findings of other workers to results obtained from the Silwood Carabidae. Finally studies were carried out on the area occupied by populations, the distribution of individuals, and the amount of movement between and within populations.

II. CARABIDAE STUDIED.

1) Review of literature and general biology.

The literature relevant to this study is extensive but diffuse. Unfortunately much of the ecological work is not necessarily applicable in Britain having been carried out elsewhere in Europe.

Lindroth (1945-49) has given accounts of the biology of many of the Silwood Carabidae in Sweden, summarising the earlier work on life histories by Larsson (1939), while Briggs (1957), Gilbert (1955, 1956) and others, have investigated life cycles of a number of species in Britain; some of the larvae are described by van Emden (1942). Van der Drift (1951) gives an account of certain aspects of the ecology of species inhabiting beech litter in Holland, and Hikimiuk (1948) and Kabacik (1957) have worked on populations of woodland Carabidae near Moscow and in Poland. Recently a number of studies have been carried out in Germany and eastern Europe on Carabidae of arable land by Scherney (1955 & 1960), Tischler (1955 (a) and (b) Thiele (1960), Geiler (1960 (a) and (b)) and Skuhravy (1955 and 1956). In particular Tischler's synecological approach appears to have stimulated a number of projects on the fauna of arable land in which Carabidae are included.

There is a large literature on activity in insects especially with regard to diurnal rhythms and the effects of temperature and other climatic factors, but little applies specifically to Carabidae. Harker (1958) has reviewed laboratory studies on daily periodicity of activity in the animal kingdom, and this has been extended to the field for several Carabid species by Williams (1959)(b)

In habit the majority of Carabidae are ground-living, being active on the surface and retiring under logs, litter or other cover, or into the top few inches of soil when at rest. Of these, some, for example Amara, Harpalus and Acupalpus species, may be swept from low-growing vegetation as recorded by Donisthorpe (1936). A few species, especially members of the genera Clivina and Dyschirius, habitually form burrows in sandy or clay soils. Demetrias atricapillus and Dromius melanocephalus fly readily and are active on the foliage of trees and shrubs, while the other members of the genus Dromius which occur at Silwood occur under, and in the crevices of the bark of trees.

That flight is limited in frequency in the majority of ground-living Carabidae is shown by the observations below, and in some such as Carabus spec' and Pterostichus madidus wings are absent and the elytra are fused in the mid-line. In others the hind wings or flight muscles are reduced, but Lindroth (1945) found that in Scandinavia many species show geographical variation in wing size. One Silwood species in which wing dimorphism is recorded in Britain is Pterostichus minor by Sharp (1913). On the Field Station, of 67 Calathus piceus examined in 1960 all were wingless, while 15 miles away near Reading 50% of this species are winged (J. Tipton, personal communication). However, this topic has not been investigated in Britain.

The only Carabidae observed in flight at Silwood were Loricera pilicornis and Bembidion quadrimaculatum. About a fortnight after emergence callow Nebria brevicollis were seen to raise the elytra but appeared unable to unfold the wings.

During the summer of 1959 a light trap was operated in an open space in woodland on Elm Hill at Silwood (see map) (Appendix). Among Carabidae taken in it were the flightless species Pterostichus madidus and P. niger which have been observed running with facility on the bark of trees, and evidently climbed into the trap. The other species found in it were Bembidion dentellum, Bradycellus harpalinus and Amara apricaria (one specimen of each) and Harpalus rufipes. The latter occurred quite frequently although not occurring otherwise in the immediate area of the trap, presumably being attracted by the light while flying; Briggs (1957) however considered that in this species flight was rare.

A suction trap for flying insects was operated from 9/5/60 to 28/8/60; it was situated in Silwood Bottom with the mouth 4 ft. from the ground. Catches of Carabidae are shown in Table 1.

TABLE 1. Carabidae in Silwood Bottom Suction Trap. 9/5/60 - 28/8/60.

Species	Catch	Species	Catch
Bradycellus harpalinus	114	Amara apricaria	2
Bembidion lunulatum	77	Bembidion 4-maculatum	2
Bradycellus sharpi	27	Amara communis	1
Acupalpus dubius	13	Clivina collaris	1
Acupalpus meridianus	4	Stenolophus teutonus	1
Trechus 4-striatus	3	Pterostichus vernalis	1
Asaphidion flavipes	2	Amara familiaris	1
Harpalus rufipes	2	Metabletus foveatus	1
Amara bifrons	2		

Thus of over 100 Carabid species taken on the Field Station only 20 have been recorded flying. Lindroth (1945) records flight in a number of

other Silwood species but the majority of his observations were made in Scandinavia, and the problem of geographical variation in wing dimorphism precludes the application of these records to the British Isles.

Aggregations of Carabidae have been recorded by a number of authors, for example in Agonum dorsale by Briggs (1956), Southwood (1956) and Allen (1957). These and other records are combined in table 2, together with a number of additional unpublished instances (Appendix 2). An aggregation is here defined as an assemblage of individuals in which all, or nearly all, are in physical contact with another individual.

TABLE 2. Carabid species in which aggregations are recorded in Britain.

Species \ Authority	Rye 1859	Cooper et al. 1928	Briggs 1956 et al.	Flint 1956	P.J.M.G.
Carabus granulatus		x			
Dyschirius spp.		x			
Eurynebria complanata					x
Nebria brevicollis				x	x
N. salina				x	x
Bembidion lampros					x
Panagaeus crux-major		x			
Harpalus affinis				x	x
Calathus melanocephalus				x	x
Calathus mollis					x
Agonum mülleri					x
A. assimile.					x
A. dorsale			x	x	x
Brachinus crepitans	x	x			x

Such assemblages show a continuous range from those described in Agonum dorsale which, from their density and frequency may have some biological significance, through those which can probably be attributed to a scarcity of suitable shelter relative to the numbers of Carabids requiring it, for example Eurynebria, Harpalus affinis and Calathus mollis, to cases, again under shelter, where no contact is achieved but the density of individuals is considerably higher than in the surrounding habitat. Examples of the last situation are:

Carabus problematicus. 1954. April. Derbyshire. Derwent valley. 11 in 2 sq. yds. of moss and litter on a rock.

Calathus fuscipes. 1960. September. Silwood Park, Berks. 6 under a single brick on cultivated ground.

Aggregation is further discussed in Nebria brevicollis (Section ~~V 2~~ C).

Carabid adults are much affected by humidity as is shown by Lindroth's (1945) emphasis on it as a property of the Carabid environment, and Thiele's (1960) observations on Abax species; Tipton (1960) and Kless (1961) were able to relate the habitats of adult Carabidae to their humidity preferenda and resistance to desiccation. Hamilton (1917) and Kern (1921) found that Carabid larvae were more susceptible to desiccation than the adults, Hamilton noting that this larval susceptibility increased at temperatures above 20°C.

The relation between temperature and the level of activity in Carabidae is discussed in Section III 2). Low temperature has an obvious and well documented inhibitory effect on rates of activity and development (Wigglesworth 1953), while high temperatures, at least in North and Western

Europe, are probably only rarely in themselves a limiting factor; Williams and Osman (1960) remark that for the majority of species in temperate climates, temperature rarely even reaches the optimum. However high temperatures may have indirect effects, for in raising metabolic and transpiration rates, increasing the insect cuticle's permeability to water vapour (Edney 1957), and lowering relative humidity they add to the desiccation risk.

2) Species recorded at Silwood.

Adult Carabidae have been collected and trapped throughout this work and the list which follows, while certainly not exhaustive, contains all the common species.

The most recent list of the British Carabidae is that of Moore (1957a) which conforms with nomenclature current in Europe and is adopted below. It differs in some respects from Kloet and Hincks' (1945) list which follows Andrewes (1931), and is widely used; however many of Moore's changes involve the rejection of Andrewes' proposals and the reinstatement of the original names of Dawson (1854), Fowler (1887), and Beare (1930), under whose arrangement many collections in Britain still stand. For example Andrewes' genus Feronia Latreille 1817 now stands under the name of Pterostichus Bonnelli 1810 of Dawson and Fowler, and Amara vulgaris (Linne 1758) has reverted to A. lunicollis Schiodte 1837. Accordingly synonyms are not included in the following list.

List of Carabidae taken at Silwood Park between October 1958 and March 1961.

Cicindela campestris L.
Carabus nemoralis Müll.
C. problematicus Herbst. ssp. gallicus Gehin.
C. violaceus Linn.
Cychrus caraboides v. rostratus (Linn.)
Leistus spinibarbis (Fab.)
L. rufomarginatus Duft.
L. fulvibarbis Dej.
L. rufescens (Fab.)
L. ferrugineus (Linn.)
Nebria brevicollis (Fab.)
Notiophilus aquaticus (Linn.)
N. palustris Duft.
N. substriatus Waterh.
N. rufipes Curt.
N. biguttatus (Linn.)
Elaphrus cupreus Duft.
Loricera pilicornis (Fab.)
C. collaris (Herbst.)
Clivina fossor (Linn.)
Asaphidion flavipes (Linn.)
Bembidion lampros (Herbst.)
B. lampros v. properans Steph.
B. dentellum (Thunb.)
B. nitidulum (Marsh.)
B. bruxellense Wesmael
B. tetracolum Say
B. femoratum Sturm.
B. quadrimaculatum (Linn.)
B. obtusum Serv.
B. harpaloides Serv.
B. unicolor Chaud
B. guttula (Fab.)

B. lunulatum (Fourc.)
T. quadristriatus (Schrank)
T. obtusus Erichson
Patrobus atrorufus (Ström)
Panageus bipustulatus (Fab.)
Badister bipustulatus (Fab.)
Harpalus affinis (Schrank)
H. latus (Linn.)
H. tardus (Panz.)
H. rufipes (Deg.)
Stenolophus teutonus (Schrank).
S. mixtus (Herbst.)
Acupalpus meridianus (Linn.)
A. dubius Schilsk.
Bradycellus ruficollis (Steph.)
B. sharpi Joy
B. harpalinus (Serv.)
Anisodactylus binotatus (Fab.)
Amara plebeja (Gyll.)
A. similata (Gyll.)
A. ovata (Fab.)
A. communis (Panz.)
A. convexior Steph.
A. lunicollis Schiödte
A. aenea (Deg.)
A. eurynota (Panz.)
A. familiaris (Duft.)
A. anthobia Villa.
A. lucida (Duft.)
A. tibialis (Payk.)
A. bifrons (Gyll.)
A. praetermissa (Sahlb.)
A. apricaria (Payk.)
A. fulva (Deg.)
A. consularis (Duft.)

A. aulica (Panz.)
Stomis pumicatus (Panz.)
Pterostichus cupreus (Linn.)
P. caerulescens (Linn.)
P. vernalis (Panz.)
P. niger (Schal.)
P. melanarius (Ill.)
P. nigrita (Fab.)
P. minor Gyll.
P. strenuus (Panz.)
P. diligens Sturm.
P. madidus (Fab.)
Abax parallelopipedus (Pill. et Mitt.)
Platyderus ruficollis (Marsh)
Calathus fuscipes (Goeze)
C. melanocephalus (Linn.)
C. piceus (Marsh)
Laemostenus terricola (Herbst.)
Synuchus nivalis (Panz.)
Odontonyx rotundatus (Payk.)
Agonum mülleri (Herbst.)
A. assimile (Payk.)
A. ruficorne (Goeze)
A. obscurum (Herbst.)
A. dorsale (Pont.)
A. fuliginosum (Panz.)
A. gracile (Gyll.)
Demetrias atricapillus (Linn.)
Dromius linearis (Ol.)
D. agilis (Fab.)
D. agilis v. bimaculatus Dej.
D. quadrinotatus (Panz.)
D. melanocephalus Dej.
Metabletus foveatus (Fourc.)

The following species have been recorded from the Field Station but have not been found during the present work:

Carabus monilis Fab. 1957. Dempster et al (1958).
Nebria salina Fairm. et Lab. } 1958. A South
Notiophilus germinyi Fauv.) Det. A. Davidson.

Moore ranks Bembidion properans as a species distinct from B. lampros, although in previous British lists the former was considered only a variety of subspecies of the latter. Lindroth (1939-40) has described differences in the aedeagus in the two forms and on external characters B. properans is distinguished by its fully developed wings and a seventh row of elytral punctures (Donisthorpe 1931), both characters being absent in B. lampros s.s. Of these the latter is extremely variable ranging from a definite row of discrete punctures to a barely perceptible linear impression; many Carabidae show a considerable range of wing development, and variation in this feature is inadequately described for British populations. The male genitalia of a number of Silwood specimens of both forms have been examined and there appears to be some variability in the distinguishing characters.

In the absence of detailed studies on the ecology of these two Bembidion forms it is felt that the differences described do not justify, without further study, separate specific status for each. Nor can B. properans properly be regarded as a subspecies as usually defined, as at Silwood it is invariably found in company with B. lampros s.s. and Fowler (1887 p. 97) records ".... It occurs not uncommonly with the type in England and Scotland". For the purpose of this thesis therefore Moore's B. properans is relegated to the rank of variety of B. lampros. It may be added that at Silwood

populations of B. lampros s.l. contained only 5-10% v. properans.

Fowler (1887) considered the allied species Amara communis, and A. convexior to be distinct, but Moore reduces A. convexior to variatal status. However Gersdorf and Kuntze (1957) figure the aedeagi of the two forms and show evident differences; specimens from Silwood and other British localities have been examined and in agreement with these authors the two Amara are here treated as separate species.

There is a list of the Coleoptera of Windsor Park, Berkshire, which lies less than one mile from Silwood, by Donisthorpe (1936); this includes all but 16 of the Carabidae recorded on the Field Station. Of these the four following, Leistus rufomarginatus (Greenslade 1961), Clivina collaris and Amara lucida (Greenslade 1960) and A. praetermissa, are not recorded for Berkshire by Moore (1957 (b)).

A. III. ASSESSMENT OF SAMPLING METHODS.

1) Introduction.

Carabidae can be sampled directly by sorting, by hand in the field, quadrats of turf or litter and the underlying few inches of soil. This method was used by Gilbert (1956) for Calathus species, by Briggs (1957) for Harpalus rufipes, and by Dawson (1957) for small fenland species of Agonum and Pterostichus, and it has been tried at Silwood. As an example of the results obtained table 3 shows the Carabidae taken in such samples between 25/7/60 and 25/8/60.

On the edges of arable land the density of Carabidae was sufficiently high to permit quantitative work, and sandy soil with an incomplete weed cover was easily worked, although for any species but B. lampros and H. rufipes a rather large sample area would be required. In grass heath the density was lower and it was found that the root system and lower stems of grasses in typical heath could only be sorted by hand at the rate of one square foot in 30 minutes. The density in woodland was quite inadequate for direct sampling.

These and other similar observations confirmed that any programme based on such a sampling method was precluded by the time it required and the destruction of the habitat involved in the relatively small area of the Field Station.

Other methods of sampling Carabidae are indirect in that they depend on the activity of individuals. Artificial cover in the form of boards and sacking was used by Gilbert (1956) and stones, logs, bricks and pieces of board were distributed about Silwood, but when visited in the day when

TABLE 3. Carabidae in soil, turf and litter quadrats. 25/7/60 - 25/8/60.

Species	Habitat		
	Arable land	Grass heath	Woodland
N. substriatus	2		
B. lampros	15		
B. 4-maculatum	3		
A. flavipes	2		
T. 4-striatus		16	
H. rufipes	13		
H. affinis	8		
H. tardus	1		
H. latus		1	
B. harpalinus	3	9	
A. binotatus	1		
P. caerulescens	2		
P. madidus	1	4	
P. minor		1	
P. niger			2
A. parallelopipedus			2
A. ovata	2		
A. familiaris	7		
A. aenea	5		
A. communis		12	
A. lunicollis		9	
P. ruficollis			1
C. fuscipes	7		
C. melanocephalus	5		
C. piceus			1
A. dorsale	1		
S. nivalis	1		
M. foveatus	1		
D. atricapillus	2		
Carabid larvae	6	15	
Total (less larvae)	82	52	6
Total area (sq. ft.)	11	20	48
Carabidae/10 sq. ft.	77.44	26.0	1.25

nocturnal species might be expected to be found sheltering under them, they proved unproductive. It appears that such cover must be left for a considerable time before becoming attractive as shelter.

The sampling method which is the basis of the present work is the pitfall trap. This has been used for studies on Carabidae by Briggs (1957), Dawson (1957), Dempster et al (1959), van der Drift (1951) and others. As used here the pitfall trap simply consists of a 1 lb. jam-jar sunk into the ground with the lip level with the soil surface. More complicated traps have been devised by Williams (1958) incorporating a device for segregating trapped arthropods according to time of capture, and by Fichter (1941) where rainwater is excluded and the catch preserved in alcohol. However, such elaboration limits the numbers of traps which can be used, and is unnecessary when frequent visiting is practicable.

Gilbert (1956) placed vertical glass screens to windward of his traps to prevent fouling by sand and dead leaves, but this reduces the catch of traps and if visited daily they rarely become choked with leaves. Initially at Silwood a glassplate was supported a few inches above the trap to prevent the entry of rainwater, but this did lead to fouling by wind-blown plant debris and was removed.

The major drawback to using pitfall traps is that the catch varies with the activity of the Carabid population, and this is discussed below in Section A III 2). However, there are other problems which are not so commonly appreciated; for example in any given period of activity a large Carabid may be expected to cover a greater distance than a smaller species, and hence stands a greater chance of being trapped. And van der Drift (1951) has described how small Carabids such as Notiophilus species can walk over

the lip of a trap only to recover balance and escape, when a heavier species such as Nebria brevicollis or a large Pterostichus would have been trapped. A demonstration of the fact that not all ground-living Carabidae are equally susceptible to pitfall trapping is afforded by experiments described below. These were devised to investigate the optimum position for pitfall traps in dense ground vegetation for various Carabid species, and the effect of trap colour on catch. Other factors which may cause unwanted variation in pitfall catches are discussed.

2) Pitfall trapping.

a) Movement and pitfall catches.

The initial aim of the following experiments was to investigate

The effect on catch of clearing vegetation from a small area around traps, and the optimum position for traps in thick tangled grassland. They also afford comparison of the catches of different Carabid species in one type of vegetation and the catches of the same species in different types of vegetation.

It was found that when a trap was visited daily over long periods the vegetation in its immediate vicinity was worn down, thus altering its efficiency and the environment of Carabidae living in the area, and the idea of clearing an area around each trap was originally conceived to overcome this.

An account is given of the results from two plots:

(1) In grass heath on the Silwood Bottom side of Elm Hill.

(2) Under a small stand of beech on Elm Hill.

Two series of supplementary observations are described.

Plot 1. In spring 1959 the vegetation consisted of dead, matted vegetation dating from the previous growing season - mainly the remains of the grasses Anthoxanthum odoratum L., Dactylis glomerata L. and Holcus mollis L., 5-6 inches deep with occasional tussocks. 9 1 lb. jam-jars were placed as in figure 1, where A, B and C are traps:

A. the lip of the jar level with the surface of the vegetation.

B. sunk in the ground within a cleared area 2 feet in diameter.

C. sunk but without a cleared area.

Trapping was carried out in two periods, one between 18/3/59 and 17/5/59 the traps being visited 28 times, and the other between 14/7/59 and 25/8/59 with 12 visits. At each visit the traps were emptied and the numbers and species of Carabidae present recorded; a few specimens were removed for identification. During the second series of observations in July and August the mass of dead grass was reduced to a depth of 3-4 inches and was bound together by fresh plant growth, the more frequent species being :

Achillea millefolium L.
Cirsium arvense Scoh.
Hieracium sp.
Plantago lanceolata L.
Ranunculus acris L.
Rumex acetosella L.
Stellaria graminea L.
Taraxacum officinale agg.
Veronica chamaedrys L.

Many species were ruderals with a rosette growth-form, and in addition there was some fresh growth of the original grasses.

Plot (2) on Elm Hill consisted of 4 traps, two each of types B and C arranged as in figure 2, in shade under beech. They were visited on 30 occasions between 18/3/59 and 23/5/59, when the ground was covered with loose litter and a sparsely distributed, recent growth of Holcus mollis and Poa pratensis L.. This contrasted with the dense, tangled vegetation of plot (1) and it was found that it allowed more Carabid movement over the surface of the ground, (see discussion of the effects of vegetation on Carabid movement).

Results. The distribution of the catch can be considered in terms of the four variables:

1) Position of trap.

2) Type of trap.

3) Type of Carabid.

4) Vegetation.

The total catches are shown in tables 1 - 3 (Appendix).

1) Position of trap. In plot (1) the traps were arranged in a Latin square to obviate large-scale effects due to spatial trends in the density of species, and observations here in Section III 2) d) suggest that the mobility of Carabidae is such that in the small area of the plot this is unlikely to be a problem. However there remain the local positional effects of grass tussocks or individual plants on the catches of traps and one object of these trials was to overcome them with traps of type B.

It has been argued that areal variation in the distribution of the Carabid population of the plot can be ignored but it is to be expected that local effects will be reflected in the catches of at least trap types A and C. Therefore the results of these experiments are not amenable to the analysis of variance, and their significance has been assessed by the X^2 test. This is confirmed by the analysis of variance of total catches (table 4).

Analysis by this method suggests that in the spring observations catch was determined by trap type, while in the summer, catches could be attributed to chance. However the analysis shows that the summer result is due to the relatively greater effect of position, that is to say catch

TABLE 4. Effect of trap position and type in determining total catches on plot 1). (Appendix tables 1 & 2).

Analysis of variance

a) 18/3/59 - 15/5/59.

Items	S.S.	D.F.	M.Sq.	V.R.	P.
Rows	93.67	2	49.35	0.97	> 0.05
Columns	18.67	2	9.35	0.02	> 0.05
Type of trap	458.67	2	229.35	45.29	< 0.01
Residual	151.9	3	50.63		
Total	728.0	9			

b) 13/7/59 - 29/7/59.

Items	S.S.	D.F.	M.Sq.	V.R.	P.
Rows	928.67	2	464.35	0.53	< 0.05
Columns	4880.67	2	2440.35	2.80	< 0.05
Type of trap	2338.67	2	1169.35	1.34	< 0.05
Residual	1745.9	3	872.95		
Total	9894.0	9			

type has less effect. But it is argued below that changes in the vegetation are responsible for the differences in the efficiency of the three trap types becoming less. It is maintained that the non-significance of the results of this analysis are due to a decrease in positional effects, with a consequent fall in the superiority of traps of type B, over the others, rather than an increase in the local effects of position.

2). Type of trap. The total number of Carabidae in each type of trap may be compared (Table 4h). It was found that traps of type B consistently trapped higher numbers of Carabidae than the others, and the cleared areas around these traps were not affected by the growth, decay or wear of the vegetation. On plot (1) in spring and summer the difference between totals for each type of trap is significant (χ^2 2 = 47.4 and 35.7 respectively; P = $<$0.001), while on plot (2) the distribution of the total catch can be attributed to chance (χ^2_1 = 1.7, P = $>$0.10).

It also showed that in spring on plot (1) traps of type C were more efficient than A (χ^2_1 = 13.33, P = $<$0.001), which suggests that more Carabid movement occurred within the tangle of vegetation than on the surface; (A was also evidently unsatisfactory in that the lip of the jar commonly projected above, or was overhung by the vegetation). However, in the summer the situation was reversed, A taking more Carabidae than C. The difference is significant (χ^2_1 = 16.P = $<$0.001) and it is concluded that the more compact mass of dead grasses (now only 3-4 inches in depth) permitted greater activity on the surface and less between it and the ground. The question of the effect of vegetation is discussed more fully below.

TABLE 4 A. Total number of Carabidae trapped in 3 types of trap.
(For explanation see text and figure 1.).

Plot (1)

(Totals for 3 traps of each type).

Type of trap / Period of trapping	A	B	C	χ^2_2	P
18/3/59-17/5/59	5	57	25	47.4	<.001
14/7/59-25/8/59	219	300	173	35.7	<.001
Total	224	357	198	56.1	<.001

Plot (2)

(Totals for 2 traps each of types B and C).

Type of trap / Period of trapping	B	C	χ^2_1	P
18/3/59-23/5/59	71	53	1.7	>.10

3) Type of Carabid. The Carabidae whose habits are known which occurred in numbers on plot (1) in the spring can be divided into two groups: the heavier ground-living species Pterostrichus caerulescens and P. madidus, and species commonly associated with plants. Amara species and Bradycellus harpalinus (these are frequently found on grasses and Donisthorpe (1936) records their capture by sweeping low-growing vegetation). These two groups were distributed as shown in table 5.

In this period small numbers occurred in A and only comparison between B and C is relevant. Type B traps took significantly more of the heavier ground-living species ($\chi^2_1 = 18.4$. $P = < 0.001$), but plant-feeding species occurred equally in both ($\chi^2_1 = 0.1$. $P = > 0.30$). This suggests that the ground-living species were moving within the vegetation and not to any large extent upon the surface, and the cleared patches of ground in B presented a larger catching area than the simple sunken traps C. Conversely Amara and Bradycellus species appear to travel on the vegetation and will therefore be trapped in C but may well avoid bare areas as in B.

The superiority of B type traps can also be interpreted in a slightly different way. Ibbotson (1958) recorded a higher catch of the Frit fly, Oscinella frit L., on sticky traps in the centre of cleared areas ranging from 4 feet to 16 feet in diameter; this he attributed to klinokinesis, due to abrupt temperature gradients at the periphery of the cleared circles. In the present case the high catch of the active Pterostichus madidus in B traps may be due to rapid turning movements after entry of the unfavourable, or at least strange, environment of the

TABLE 5. Numbers of two types of Carabid taken in each type of trap. Plot (1) 18/3/59 - 17/5/59.

Type of Carabid \ Type of trap	(A)	B	C	χ^2_1 (B and C)	P
Heavier ground-living species	(3)	31	5	18.4	<.001
Species associated with plants	(2)	17	16	0.1	>.30

cleared areas, while the slower-moving Amara and Bradycellus species tend to penetrate no further than the edge of the cleared area and are thus less liable to be trapped in it.

The same comparison cannot be made for plot (2) or for plot (1) in the summer as in neither case were more than occasional Amara or Bradycellus trapped. However, in plot (1) in July and August a number of other species occurred which are known to be plant-feeders (Davies 1959) and their distribution can be compared with that of Pterostichus madidus, the only abundant heavy ground-living species at the time. The phytophagous species are rather mixed, including the relatively large and sluggish Harpalus rufipes and Pterostichus melanarius, and smaller, fast-moving species such as Calathus fuscipes and C. melanocephalus. Catches of the two groups are shown in table 6.

Here again for the large non-phytophagous species type B are more efficient ($\chi^2_2 = 64.66$. $P = < 0.001$) although the difference between A and C is slight. However, the distribution of the phytophagous species can be attributed to chance at the 0.05 probability level ($\chi^2_2 = 5.28$. $P. = > 0.05$), which again suggests that this group showed more surface activity than Pterostichus madidus. However, it is an artificial grouping, and if the larger Harpalus and Pterostichus species are considered alone it is seen that the distribution is even more uniform, while the more agile Calathus species show a low catch in B ($\chi^2_3 = 7.3$. $P = 0.05$). It is probable that only the latter can properly be regarded as moving mainly on the surface of the vegetation, especially as the large Harpalus species and Pterostichus melanarius seem to feed largely on fallen plant seed (Briggs 1957 and Davies 1959).

TABLE 6. Numbers of types of Carabid taken in type of trap. Plot (1) 14/7/59 - 25/8/59.

Type of trap / Species	A	B	C	χ^2_2	P
Pterostichus madidus	155	263	136	64.66	<.001
Pterostichus melanarius	6	6	9		
Harpalus rufipes	1	8	4		
H. latus	1	1	1		
Total - heavier plant-feeding species.	8	15	14	2.33	>.30
Calathus fuscipes	5	9	23		
C. melanocephalus	14	3	5		
Bradycellus	-	-	1		
Total - lighter plant-feeding species	19	12	29	7.3	<.05
Total - plant-feeding species.	27	27	43	5.28	>.05

But whatever the causes of this differential trapping of various species, the point here demonstrated is that different types and species of Carabid will be trapped in different proportions in any given type of trap.

4) Vegetation: Pterostichus madidus formed a high proportion of the total catch throughout these experiments and the numbers in the different traps can be compared for spring and summer on plot (1) and for spring on plot (2) (table 7). In spring on plot (1) B took significantly more of this species than the other types of trap ($\chi^2_2 = 26,66$ $p = < 0.001$) and it has been suggested above that this was due to a high proportion of activity taking place within the vegetation, and this difference persisted later in the summer ($\chi^2_2 = 64.66$ $P = < 0.001$). On plot (2), however, the superiority of type B traps was less marked (although present when P. madidus is considered alone), ($\chi^2_2 = 5.40$ $P = < 0.05$) and this is attributed to the sparser ground vegetation here allowing more freedom of movement over the surface of the ground.

If the total catches of the various types of trap on plot (1) are compared in spring and summer (table 4) the larger proportion in type A in the latter period implies more activity on the surface of the vegetation, but it has been suggested that this was due to the appearance of surface-living Carabidae such as Calathus species rather than to any change in the habits of the persistent species. This is confirmed by the distribution of Pterostichus madidus (table 7) which shows a significantly higher catch in B in both seasons. Apparent differences in the occurrence of this species in the two seasons when A and C are compared can be tested by treating this data as a contingency table applying Yates' correction for

TABLE 7. Numbers of Pterostichus madidus taken in each type of trap.

Plot \ Type of trap	A	B	C	χ^2	P
(1) Spring	3	26	5	χ^2_2 28.66	<.001
(1) Summer	155	263	136	χ^2_2 64.66	<.001
(2) Spring	-	47	27	χ^2_1 5.40	<.05

continuity:

$$\chi^2_1 = 0.272$$

$P = > 0.50$. Thus there was no significant change in the relative efficiency of traps of type A and C with changes in the vegetation between the spring and summer observations. However, a similar test can be applied to the data including type B traps:

$$\chi^2_2 = 11.17$$

$P = < 0.001$. Type B traps therefore were (compared with A and C) more efficient at trapping Pterostichus madidus in the spring than in the summer.

It has been argued that there were no changes in the behaviour of Pterostichus madidus between the spring and July-August; and therefore the above differences in relative effectiveness of B traps between the two periods must be due to changes in the vegetation. This is to be expected considering the compaction of the dead plant material in the areas as the year progressed.

Thus different types of vegetation may affect the trapping of a Carabid species (as shown by the relative efficiency of type B traps in the spring in tangled, dead grasses compared with a sparse, new erect growth), and there may be trapping differences in the various annual phases of a single vegetation type (for example when the efficiency of B type traps on the grass heath is considered in spring and later summer).

These variations in the efficiency of traps caused by differences in the physical characters of various types of grassland are slight, but their

presence implies that there will be a greater discrepancy between the proportions of populations of the same species trapped when two more diverse types of substrate are compared, for example a thin layer of beech litter and the tangled heath vegetation of plot (1).

Rate of movement of Carabidae.

Further evidence of the effect of the vegetation or ground cover on the ease of movement of Carabidae and hence numbers trapped, is provided by a transect of traps in South Lodge Wood in early summer 1959 which is discussed in detail in section B II.

5 traps were spaced at 12 foot intervals in a straight line; the ground was covered in beech litter except in the middle of the transect which was crossed by a bare sandy track. The depth of loose litter was measured at 5 points within a radius of 6 feet of every trap and the means of these values can be compared with the total number of woodland Carabidae taken in each.

Figure 3 shows that the catch varied inversely with the depth of loose surface litter. This applies to the total of woodland Carabidae taken in each trap but Nebria brevicollis, the most abundant species, may be considered alone. Over the small area covered by the transect the high catches in the middle cannot be attributed to a locally high population of Carabidae, but can be explained by the absence of litter here allowing greater freedom of movement, and hence a greater likelihood of any individual Carabid being trapped.

Attempts were made to estimate the relative rates of movement of different species in a given vegetation, and of the same species in

different types of vegetation.

Metal sheeting strips 6' 2" x 10" were used to enclose plots 6' x 6' on beech litter in South Lodge Wood, and on grass heath on Elm Hill; the strips were embedded 3" in the soil, and at the corners of the plots the strips were pegged tightly together. Within each plot one pitfall trap was sunk.

Known numbers of various Carabid species were liberated in each plot to compare rates of recapture. Unfortunately no conclusive results were obtained as Carabidae released rapidly escaped; this was indicated by the recapture of marked individuals outside the plots, and by estimating the numbers within by marking. This was found for all the species used: Nebria brevicollis, Pterostichus madidus, P. niger, P. melanarius, Abax and Harpalus affinis.

Van der Drift (1951) also reported difficulty in confining Carabidae within plots.

DISCUSSION.

The experiments described show that clearing vegetation from a small area around pitfall traps limits the effect of wear on vegetation through frequent visiting, and to some degree standardises traps situated in different types of ground cover, especially when grass tussocks are present. It was also found that the cleared traps gave a consistently higher catch of Carabids than the other types tested. However, in the case of phytophagous species and those active upon the surface of the vegetation traps without a cleared area may be as, or more efficient than those with one; in the aggregate catches for each type of trap this is obscured by the relatively

larger numbers of such ground-living species as Pterostichus madidus. However, it is with the latter type of Carabid that this study is mainly concerned and traps with a cleared area were adopted for all sampling.

These experiments afford a demonstration of the point already mentioned, that the efficiency of pitfall traps varies with species of Carabid; while this is obvious when extremes such as Carabus and Notiophilus species are contrasted, it also holds for species which are superficially closer in size and activity, for example Pterostichus madidus and Calathus fuscipes. Therefore these traps should not be used for the quantitative estimation of the species comprising the Carabid fauna of any habitat.

A. III. 2)

(b) Behaviour and pitfall catches.

Van der Drift (1951) commented on the ability of diurnally active Notiophilus individuals to evade capture by pitfalls, and Williams (1959b) found that these traps did not give a representative sample of the numbers of this genus. These and other diurnal species have well developed eyes and probably see and avoid traps. A similar impression was gained at Silwood for hand collecting and pitfall trapping in any area frequently showed a discrepancy between the numbers of diurnal species taken by the two methods. Daily cycles of activity are described later (Section B III) and the Carabidae taken in soil samples on cultivated land (table 3) can be divided into three groups: diurnal, nocturnal, and those which frequently have been recorded as active both in the day and night. Those taken in pitfall traps over the same period (25/7/60 - 25/8/60), and in the same area (Hill Bottom), can be similarly divided (table 8).

TABLE 8. Numbers of Carabidae of three types of daily activity cycle, taken in soil samples and pitfall traps.

	Diurnal	Active day and night	Nocturnal	Total
Soil samples	36	13	33	82
Pitfall traps	26	16	70	112
$\chi^2_{[1]}$	10.78	P =	< 0.01	

If those species active both in the day and night are excluded from the comparison, the significance of the difference in the proportion of diurnal and nocturnal individuals taken in soil samples and pitfall

traps may be tested by treating the data as a 2 x 2 contingency table. This shows that pitfall traps take a significantly lower number of diurnally activ. Carabidae than would be expected if all species were trapped according to their absolute density.

An attempt was made to render traps less easily seen by diurnal Carabidae, by painting jars white, thus making the tone of the shadowed interior of the traps lighter and closer to that of the general ground surfac around it. The catches of such traps were compared with those of black-painted ones.

Nine traps, three white, three black and three unpainted controls arranged in a Latin square, 4 x 4 yds., were visited daily between 4/5/60 and 24/5/60. They were situated on bare soil with a sparse weed cover in Hill Bottom. Appendix table 4 shows detailed catches, which are assigned to activity groups in table 9 below.

TABLE 9. Catch of Carabidae in white, black and unpainted pitfall traps.

Trap	Diurnal	Active day and night	Nocturnal	Total
1 B	2	1	0	3
2 W	9	7	2	18
3 C	6	2	1	9
4 W	6	21	3	30
5 B	5	5	3	19
6 C	6	9	2	17
7 W	12	9	0	21
8 C	22	7	1	30
9 B	5	3	3	11

The analysis of variance of the factors determining the catch of diurnal species in table 9 is shown in table 10.

TABLE 10. Catch of diurnal Carabidae in painted and unpainted traps.

Analysis of variance:

Items	S.S.	D.F.	M.Sq.	V.R.	P.
Rows	107.56	2	53.78	6.40	> 0.05
Columns	69.56	2	34.78	4.14	"
Type of trap	56.56	2	28.28	3.36	"
Residual	25.21	3	8.40		
Total	258.89	9			

This experiment therefore affords no evidence that either the colour or position of traps in the plot had any effect on the catch of diurnal Carabidae. This is perhaps best attributed to the behaviour of the diurnal species, for in the field diurnal members of the genera Notiophilus, Bembidion, Amara and Metabletus can be seen moving rapidly for short distances and then pausing, and during such pauses may become aware of pitfalls.

c) Weather and Activity.

Between early October 1958 and the end of July 1959 23 permanent traps were visited as far as possible daily, between 0900 and 1100 hours G.M.T. (B.S.T. in the summer). During this period Carabid activity is negligible as the observations on daily rhythms (Section B III) indicate. The daily catch, therefore, resulted from the activity of nocturnal species in the previous night and of diurnal ones throughout the day after the last visit.

It was found that the catches of Carabidae showed considerable variation and this can be attributed to changes in climatic factors. The daily catches in the 23 traps for summer 1959 are shown in figure 4 and Appendix table 5. Williams (1940) showed that the activity of insects caught in a light trap was affected by a number of factors including temperature, windspeed, rainfall and humidity, and the daily catches of Carabidae have been compared with the Silwood meteorological records. Diurnal and nocturnal species will obviously respond to different factors, for example the activity of the former is liable to be affected by the daily maximum temperature, and the latter by the minimum.

In the 23 traps the total catch on any day was small and separation of diurnal and nocturnal species reduces the totals to an unworkable size. However, from 26/6/59 until 30/7/59 the end of summer trapping, a further 13 traps were visited daily, 11 in woodland and grass heath on Elm Hill and 2 in Hill Bottom, and their daily catch has been added to that of the other traps.

Strictly diurnal species comprised only 12.5% of the catch over this period, and the relation between nocturnal activity and weather is considered after subtracting diurnal species from each daily catch. Pterostichus madidus is retained in the nocturnal group here, as although it may be diurnally active it was a common species in the summer and must have contributed a large proportion of the nocturnal activity.

It was found that the fluctuations in numbers compared best with the Silwood screen grass minimum temperature (figure 5) which usually occurred in the early hours of the morning after or towards the end of the

period of activity of nocturnal Carabids. Daily readings of the temperature were taken at approximately 0930 hours (B.S.T.), and the values obtained on any day corresponded with the catch of Carabidae that morning.

The traps were not visited between 12/6/59 and 16/6/59, and on 9/7/59 heavy rain resulted in the flooding of many traps. Between 6/6/59 and 30/7/59 a positive correlation was found between grass minimum temperature and catch at the 0.05 probability level (table 11). This period was divided into two parts each of 24 days to allow for changes in total Carabid populations and the correlation coefficient for number and grass minimum was calculated for each:

6/6/59 - 3/7/59 $r = 0.595$ $P = > 0.01$

4/7/59 -30/7/59 $r = 0.680$ $P = > 0.001$

In the winter months (December to February inclusive) Carabid activity was slight, only occasional specimens of Nebria brevicollis, Notiophilus species, Pterostichus madidus and Bembidion lampros being taken in the 23 traps. With the exception of Nebria these are largely diurnal species and may have been stimulated into activity by high afternoon temperatures, and the inference is that in the winter months low night temperatures prohibit Carabid activity; but their absence from the traps may also be due to low adult populations of the preponderant larval-overwintering species, or diapause in the adult over-wintering ones.

The traps were scattered between Pond Field, South Lodge Wood, Elm Hill and Hill Copse and few of the climatic factors of which routine measurements are made at Silwood can be presumed to vary sufficiently

TABLE 11. Correlation between catch of Carabidae and Grass minimum temperature.

Date	No.	Grass Min. °F.	Date	No.	Grass Min. °F.
June 6	32	46.5	July 6	34	48.0
7	31	49.0	7	36	47.0
8	31	48.0	8	49	43.0
9	23	45.5	9	42	46.5
10	27	46.0	10	Many traps flooded	
11	20	42.0	11	35	55.0
12)			12	33	48.0
13)			13	17	43.0
14)			14	19	34.0
15)	Traps not visited		15	19	38.5
16)			16	22	38.0
17)			17	56	49.0
18	19	48.0	18	49	45.0
19	14	43.5	19	25	35.0
20	23	46.0	20	14	38.5
21	13	48.0	21	39	46.0
22	28	54.0	22	59	47.5
23	33	57.0	23	32	45.5
24	30	51.5	24	20	44.5
25	50	59.0	25	37	45.0
26	39	56.0	26	30	44.0
27	54	56.5	27	59	52.0
28	35	58.0	28	46	48.5
29	26	51.0	29	55	46.5
30	24	51.0			
July 1	17	40.0			
2	39	56.0			
3	54	50.0			
4	44	47.0			
5	43	47.0			
No. of observations	24			23	
r	0.595			0.680	
P	< 0.01			< 0.001	

regularly to be related to trapping over this area; for example windspeed and humidity near the ground vary greatly with small differences in topography and vegetation as Wilson (1959) has shown.

On some occasions rain was followed by a high catch of Carabids the next day which could not be attributed to any increase in temperature. However on 26 occasions between the beginning of April and the end of July 1959 trapping coincided with recorded rainfall. This was associated with a fall in grass minimum temperature (as compared with that of the previous day) 13 times, with a rise 11 times, and twice there was no change; out of the 26 days the catch of Carabidae fell 14 times and rose 12. In this case there was no apparent relation between activity and rainfall, although during this period rain was unusually light and infrequent.

Here no attempt is made to segregate the effect of the various climatic factors, although Williams (1940) showed that for a light-trap:

log. catch = log. activity T + log. activity H.....
+ log. population .

Where log. activity T is activity due to, or permitted by temperature; log activity H activity due to humidity..... Hughes (1956) has demonstrated a method of separating the effects of the different climatic factors which affect the activity of an insect. It is therefore theoretically possible to correct for variations in catch due to activity if changes in climatic factors are known, thus obtaining from pitfall traps a value for Carabid population. However, Williams also found that in terms of amount of activity the response to a given change in temperature varies for the same insect species at different times of the year;

similarly Perthunnen (1952) found that the humidity reactions of the earwig Forficula auricularia showed seasonal changes. Mellanby (1939, 1940, 1958) and Colhoun (1960) have shown that insects acclimatise to temperature and Falconer (1945) found that activity at any temperature varies with the temperature at which the insect was conditioned; the work of Nicholson (1934) emphasised the importance of change of temperature, rather than the foregoing and resultant steady levels, on activity. When the effects and interactions of other climatic factors were also considered it was evidently impractical, at least in the present work, to attempt to reduce the effect of weather on activity to a simple equation.

d) Trap density and catch.

To test the effects of the distance between traps in a plot on the catch, three unenclosed plots were laid out in a level area of beech-litter in South Lodge Wood. Each consisted of 8 traps arranged in a square with a ninth in the centre, as in figure 6; the three plots were 12 x 12 ft. in plot X, 6 x 6 ft. in Y and 3 x 3 ft. in Z. The distance between plots (15 ft.) was greater than that between traps in any plot (maximum 6 ft.), but X, Y and Z were placed sufficiently close together for it to be assumed that they were sampling the same Carabid populations under the same conditions. In fact, using Williams' (1947) Index of Diversity, there was no significant difference in the Carabid fauna of the three plots.

The traps were visited regularly between 6/5/59 and 6/6/59, and the total catches are shown in Appendix table 6. Nebria brevicollis constituted

94% of the total and table 12 shows the catch of this species.

If the presence of the outer traps has no effect on the numbers of Carabidae taken by the central ones, the catch of the latter can be expected to approximate to the mean of the total catch for all the 9 traps in a plot. If the central trap takes appreciably less than this mean it can be concluded that the outer ones are cutting off some of its potential catch. The catches of the inner traps and plots are compared (χ^2_1) in table 12 for Nebria brevicollis.

It was found that the catches of the inner traps were not significantly reduced by the presence of the outer ones. In addition, there is no relation between the mean: inner trap ratio and the distance between traps thus the density of traps seems to have no effect on catch. These observations suggest a Carabid population (consisting almost entirely of Nebria brevicollis) of extremely mobile individuals, but as problems of finding suitably extensive areas of uniform beech litter did not permit replicated experiments or larger plots this argument cannot be pursued.

It is noticeable that in each case the inner trap catch is lower than the mean, although the difference is not significant. This may indicate that in a more extensive trap system of traps there would be a significant reduction in the centre, or it may be a reflection of the spatial distribution of Carabidae.

The numbers of Nebria brevicollis taken in each trap are shown in figure 7. The highest catches occurred around the further corners of plots X and Z centred on traps 3 and 1 respectively. During the course of this

TABLE 12. Comparison of the catch of Nebria brevicollis in inner and outer traps on plots X, Y and Z.

PLOT	X	Y	Z
Total Nebria in plot	185	195	202
Mean	20.56	16.11	22.25
Nebria in inner trap	16	11	17
χ^2_1	1.01	1.62	1.24
P	$> .30$	$> .20$	$> .20$

experiment Nebria was emerging from pupation and hibernation sites (see Section B I). Traps 1, 2 and 4, plot 2, coincided with a particularly deep patch of litter and trap 3, plot X was the nearest trap to a Rhododendron bush 10 ft. away. It is possible that these two sites were refuges from which a high proportion of the active Nebria population originated.

It was concluded that the lower than average catches of the inner traps and the relatively low catch in plot Y were due to the distribution of Nebria brevicollis and not to any interaction between traps or plots. Therefore, throughout this work traps have been placed at the most convenient density, and in fact this has almost invariably been lower than the density of traps in plot X.

e) Baited traps.

There is some evidence that certain Carabidae are attracted to carrion; for example, a large number of species occurred in carrion-baited pitfall traps operated by Walsh (1931) and Kaufman (1937), but many of these may have been adventitious. However, Dawson (1957) using unbaited traps which were visited infrequently found that significantly more Agonum and small Pterostichus species were taken by those in which small mammals had died and decomposed. Kabacik (1957) used baited traps to sample Carabus arcensis Hbst. and Pterostichus niger but found reactions to bait extremely variable.

4 2-lb. jam-jars were sunk in a level beech litter-covered area on Wood Bank, arranged in a 3 ft. square with diagonally opposite traps baited with raw fish. The experiment was continued from 13/4/59 to 9/7/59, the traps being visited 41 times.

Carrion beetles, especially members of the genera Tachinus, Creophilus, Philonthus, Aleochara, Omalium, Necrophorus, Oeceoptoma, Catops and other Cholevidae and Histeridae, were abundant in the baited traps, but these took no more Carabidae than the unbaited. Of the total 175 Carabids recorded in the traps 42 were Pterostichus madidus, which is often a scavenging species, and one of the most frequent Carabidae in carrion, but even here the same proportion occurred in the baited as in the unbaited traps (baited traps - 20, unbaited - 22).

As a result of this no further work on baiting Carabidae has been attempted.

3) Discussion.

Direct quadrat sampling of Carabidae, baited and camoflaged traps have been dismissed, and attention concentrated on simple pitfalls. Ideally the catches of such traps should be capable of quantitative comparison with catches from other areas and vegetation types at the same time, and with catches from the same area at other times. However it has been demonstrated that catches are affected by daily variations in activity due to weather and by the resistance to movement imposed by the vegetation cover. To some extent the effects of climatic fluctuations can be allowed for by using total catches for several days or weeks, and if the main concern lies in comparing the relative numbers of one or more species in different parts of an area, by restricting comparison to simultaneous trapping periods. However there remains the vegetation factor which entails further restriction of sampling to a single plant community.

It has also been shown that pitfall traps are selective in that populations of different species, from their behaviour, tend to be trapped in differing proportions. It has been suggested that various species and life forms have their own strata of activity in thick grass heath, and Kabacik (1957) found that Carabus arcensis moved only on or near the surface of litter, while Pterstichus niger may be active both on and within it. Furthermore diurnal Carabidae show discontinuous movement, and with relatively well developed powers of vision are less easily trapped than nocturnal species.

From this one must conclude that pitfall traps should not be used for the quantitative estimation of the Carabid fauna of any habitat; nor

should they be used for comparing the numbers of the same species in different habitats as various types of ground cover present different degrees of resistance to Carabid movement. In addition, there are indications that seasonal changes within a vegetation type due to plant growth and decay may affect the trapping of Carabidae. But it has been taken that the presence of cleared areas around traps does permit the comparison of catches of a species within a single type of vegetation at any one time.

Fichter (1941) however, discussing pitfall traps, states that they may be used to compare the "..... composition of soil surface arthropod populations in two or more habitats". But for quantitative work this is evidently untrue, especially if it embraces groups more diverse than a single family of Coleoptera.

Boyd (1960) used pitfall traps to compare the surface active invertebrate fauna of grazed and ungrazed maritime grassland on the premise that "..... Pitfall catches probably give a fairly accurate indication of the surface activity of the soil fauna." The comparison was between closely cropped grassland and an ungrazed sward which reached ankle-depth, and while the results showed distinct qualitative differences in the fauna of the two areas, it is questionable whether any quantitative comparison is permissible.

Williams (1959a) used pitfall traps to measure the activity of ground-living invertebrates in different habitats interpreting the catches of traps as measures of the level of activity in their respective vegetation types. However catch represents locomotor activity expressed as movement in a

horizontal plane, and for any given energy outlay the amount of such movement will be greater in an essentially two-dimensional habitat, for example a thin layer of beech-litter, than in a three dimensional one such as plot (1) in its spring aspect.

After using pitfalls to compare the Carabid fauna of various field crops Scherney (1960) concluded that Carabidae are "followers of cultivation". He found that pitfall catches on densely weed-covered waste ground were $\frac{1}{10}$ those on wheatfields, $\frac{1}{8}$ of those in barley, $\frac{1}{7}$ of the catches in potatoes, $\frac{1}{5}$ of those in clover, and $\frac{1}{3}$ of grass meadow catches. His conclusion may be valid, for table 3 shows maximum Carabid density on the edges of arable land. However, it is noticeable that the sequence of increasing Carabid abundance (in traps) from meadow and rank vegetation to cereal fields, is also a sequence of decreasing resistance to the passage of Carabidae over the ground surface.

These examples illustrate the fact that pitfall captures must be used for comparative purposes with discretion. It is however theoretically possible to make allowances for the short-comings of pitfall traps. A detailed analysis of daily captures in relation to fluctuations in climatic factors would permit correction for the effect of weather on activity, while comparison of the catch of different species in any type of vegetation, or of the same species in different vegetation types may be possible after work on the lines of the unsuccessful enclosure experiments already described. Thus corrections could be made for the majority of factors causing variations in activity, and it would then be possible to use pitfall catches as measures of the absolute densities of various populations, within the limits of

accuracy of the activity correction made, after the estimation of the numbers of one species by some other method.

However the difficulty of calculating the appropriate correction in the case of daily variations due to climatic factors has been mentioned. This requires continual measurements of the microclimate, and although the latter should be considered at some stage of any investigation into Carabid habitat and distribution the assessment of temperature and humidity at the ground surface in grassland or on bare soil poses a number of technical problems whose solution is irrelevant if the initial aim is only to describe the pattern of distribution of populations. In addition there remains the problem of seasonal variation in the activity of species.

Alternatively the drawbacks of pitfall traps in comparing relative numbers in different situations can be overcome by direct estimation of absolute populations by marking and recapture, when the inefficiency of the trapping method is immaterial so long as adequate numbers are taken. Some idea of the distribution of populations is provided by remarking recaptured individuals and obtaining estimates of migration to and from plots, recording the direction and distance of movement by marked Carabids, and in using pitfall trap catches as indicative of density. Here variations in activity are largely ignored and attention is concentrated on release and recapture, using uncorrected pitfall catches to indicate general distribution. At first this involves considerable lack of precision in the determination of relative densities in different parts of a fairly uniform area, over a gradient of an environmental factor, or in adjacent but different vegetation types. However, as information on movement and absolute and relative

densities accumulates a higher degree of accuracy can be achieved, and the most imprecise initial observations contribute something to the total.

At some stage in the work it is necessary that factors influencing activity be studied in order to relate observed distances moved by individuals to the general level of activity in a population as indicated by pitfall catches. Similarly analysis of the reasons for distributions observed requires investigation of the microclimate but this work can be restricted to critical factors or parts of the habitat, and at such a stage there would be justification for the additional labour involved in a limited amount of direct sampling. However this goes beyond the scope of the present study. Here it has proved most profitable to accept the limitations and inaccuracies of pitfall trapping, and to consider the effect of the microclimate and the reasons for an observed level of activity only when necessary, rather than to embark immediately on a detailed quantitative analysis of the factors determining Carabid activity.

Pitfall traps are used in this work to sample and compare the Carabidae of distinct vegetation types, but the catches have been checked by extensive collecting and field observation, and in fact faunas are described which can usually be distinguished by the presence or absence of indicator species.

B. ASPECTS OF THE BIONOMICS OF SPECIES

I. LIFE HISTORIES AND ANNUAL CYCLES OF ADULT ACTIVITY.

1) Introduction.

The annual cycles of Carabidae considered here and other common species which have been worked out in Britain include Harpalus rufipes and H. affinis (Briggs 1957), Notiophilus species (Davies 1955 and 1959), fenland species of Agonum and Pterostichus (Dawson 1957), Nebria brevicollis (Gilbert 1958 and Williams 1959b), and Calathus fuscipes and C. melanocephalus (Gilbert 1956). Van der Drift (1951) investigated Carabus violaceus, C. problematicus, Pterostichus and Abax parallelopipedus in Holland.

The life histories of many other Silwood species have been described in Scandinavia by Lindroth (1945 and 1956a) and Larsson (1939), but their accounts do not necessarily agree with the actual cycles in Britain. For example these two authors state that Calathus fuscipes and C. melanocephalus are both autumn breeders with similar cycles, but Gilbert (1956) found that in North Wales there were distinct differences in the annual distribution of adult activity in the times of emergence, mating and egg-laying, and in the number of adults overwintering.

The life histories of 26 species common at Silwood are considered here;in some cases the numbers taken in pitfall traps hardly merit their inclusion; examples are Notiophilus species and Loricera, but these are more numerous than pitfall captures suggest, and form an important part of the Carabid fauna. Others, especially Synuchus nivalis, were abundant in 1959 but extremely rare in 1960. Cychrus, Leistus ferrugineus and Stomis

are included as they are used subsequently to define Carabid faunas of certain seasons and vegetation types, and L. ferrugineus also shows a life history of some inherent interest.

All larvae taken during this work by collecting in pitfalls, or soil quadrats, have been recorded but they have not been studied in detail as many groups are not susceptible to specific identification and others require laborious direct sampling methods.

Detailed studies on populations of Nebria brevicollis and Pterostichus madidus are described in Section C and therefore the life histories of these species are dealt with separately; the annual cycle of the latter does not appear to have been described previously in detail.

Cycles of adult activity as shown by pitfall catches are compared with what would be expected from British, or in their absence Scandinavian or other accounts of the life histories. Where recorded in significant numbers reference is made to the occurrence of larvae and callows.

Data on adult activity are derived from the following series of traps:

23 traps generally distributed over the S.E. part of the Field Station in woodland and grassland.

October 1958 - November 1959.
March - November 1960.

11 traps on Elm Hill, woodland and grassland.

May - November 1959
March- November 1960

2 traps in Hill Bottom. Arable land.

May - September 1959.

3 traps in Hill Bottom. Arable land.

April - November 1960.

50 traps on Wood Bank. Woodland.

April - November 1960.

36 traps on Elm Hill. Grassland.

June - September 1960.

For all species except N. brevicollis and P. madidus results are shown in figure 12 and Appendix tables 8 - 15, and for all species except these two (and except where shown otherwise in figures and tables) catches are expressed as 10 x mean catch/day for 14 day periods. On three occasions the 23 traps were only emptied at irregular intervals giving one unit of 21 days (December 1958), one of 28 days (March-April 1959), and one of 24 days (August 1959).

2) Description of life histories.

a) Nebria brevicollis. The life history of this species has been described in Britain by Gilbert (1956) and Williams (1959); it breeds in the autumn and overwinters as the larva. Newly emerged adults appear from May to June, show some early summer activity but diapause until the main period of reproductive activity in the autumn from September to November.

At Silwood the life history was similar; adults were trapped in large numbers in October (figure 8) and towards the end of the period mating occurred. First instar larvae appeared in laboratory cultures in November, and in the field until April, while later instars were found in traps and litter throughout the winter months and in early spring. In April and May pupae could be obtained by digging to a depth of 1-2 inches in bare sandy places in woodland. From April until June callow adults were trapped, being recognised by their pale colour and soft integument and the numbers occurring in traps are shown for 1959 in table 13.

In 1959 the first callow was recorded on April 13th and there was a rapid increase at the end of the month. They formed the maximum percentage of the Nebria taken in traps between May 1st and 8th, while between May 12th and June 8th the total numbers in traps reached a peak. The period of approximately 20 days between these two maxima agrees with the two to three weeks required in the laboratory for the palest Nebria specimens found to attain mature colouring and a hard integument on the dorsal surface of the body.

The ventral surface of a newly emerged adult may remain soft several weeks after its dorsum has become indistinguishable from that of a mature

individual and it is of interest that Dawson (1957) found that aedeagi of Agonum obscurum and A. fuliginosum may remain unsclerotised up to six months after emergence. In the autumns of 1958, 1959 and 1960 occasional Nebria were found which showed signs of immaturity on the under-side, but they were probably late developing or emerging individuals from the spring, and did not occur in numbers large enough to invalidate the concept of spring emergence, summer diapause and autumn activity.

At Silwood the immediate post-emergence activity is greater than Gilbert's (1956) figures would suggest, but in both 1959 and 1960 the maximum May and June catches were approximately half those of the autumn (figure 8). In contrast, at one locality near Reading, Berks., Williams (1959) records spring catches higher than those of the ensuing autumn, and cites Lindroth (1945) as giving a bimodal curve for the occurrence of N. brevicollis adults in Sweden, with the spring numbers greater than those of the autumn. In Denmark he quotes Larsson (1939) as describing a single peak. The relation between level of summer activity in Carabidae and latitude is further discussed below in Section B I 3).

b) Pterostichus madidus. The life history was investigated between October 1958 and May 1961 by sampling adults in pitfall traps; the occurrence of larvae and callows was recorded and in 1960-61 seasonal changes in the sex-ratio and condition of the female gonads were studied. This is one of the most universal British Carabidae yet its low density (< 1/sq.yd. in 1960 (Section C)) precluded direct sampling; changes in absolute population estimates obtained by marking and recapture are discussed later (Section C).

TABLE 13. % Callow (immature) Nebria brevicollis adults in pitfall traps - April-June 1959.

Trapping Period	Total No. Nebria.	No. Callow	% Callow
April 23-26	15	0	0
" 27-30	32	1	3.1
May 1-4	29	19	65.5
" 5-8	57	37	64.9
" 9-11	36	21	58.3
" 12-15	86	32	37.6
" 16-19	28	9	32.1
" 20-23	56	20	35.7
" 24-27	18	4	22.2
" 28-31	43	2	4.7
June 1-4	73	5	6.8
" 5-8	75	2	2.7
" 8-11	47	0	0
Totals	594	152	

Pitfall catches of adults in 1958-59 are shown in figure 9; they were present almost throughout the year with a well-marked peak during July and August, when copulation was frequent. The population estimates in Section C demonstrate maximum activity and numbers during this period. Catches fell throughout the winter reaching a minimum in February and March.

Larvae of this species were found only infrequently in traps, but they have been recorded in soil, turf and litter from September until June. In P. madidus the adults are inactive until the integument has acquired the mature black colour and newly emerged individuals could be recognised only occasionally by the flexibility of the elytra; they were recorded in this condition in June, July and early August.

From these observations it appears that the main period of activity occurs in July and August when the eggs are laid; the species overwinters in the larval state and new adults emerge in the following summer; some of these survive into the winter and may enter a second season.

In 1960 changes in the sex ratio were determined in those P. madidus taken in a large number of pitfalls (figure 10). Also shown are the mean daily catches of male and female P. madidus in the 23 traps (Appendix table 7). From the figure it is evident that males emerge from May onwards reaching a maximum in July and August; after this the majority die, a few surviving into the autumn; (collecting reveals occasional winter females but rarely males). A number of females overwinter in the adult state reappearing in May and June; the new generation emerges at the same time as the males and hence the double peak in female catch.

Samples of females were taken from traps at irregular intervals from June to early November 1960 and the ovaries were dissected after preservation in 70% alcohol. The length of the right ovary was measured to 0.5 mm, and the condition was assessed as:

Immature. (less than 4 mm. in length, individual ova indistinguishable to the naked eye).

Mature. (more than 4 mm. in length, individual ova distinct, the largest usually not less than 2 mm in length.)

Spent. (Eggs laid, as shown by the presence of corpora lutea, the oviducts being expanded but empty, or having collapsed or disintegrated).

In early June it was possible to distinguish between those females which had laid in the previous season, and immature individuals which had not. Unfortunately it was not possible to recognise any females which had reached maturity in a second season, as the egg masses filled the oviducts.

Results are shown in figure 11 as fortnightly means. No samples were taken in the first half of September.

In agreement with the suggestion of a main breeding season in July and August the percentage of reproductively immature females was high in June falling steadily until October, while the percentage of spent females rose. In the autumn there was an increase in the proportion of immature individuals so that the population entering the winter consisted of 25% immature and 75% spent individuals. During the winter of 1958-59 occasional pitfall catches of P. madidus females were made suggesting that there was no diapause and activity was limited only by weather. Thus the fall in catch between autumn and spring, (from a maximum of 2.5/day in

October 1958 to 0.5/day in March 1959, and 0.5/day in October 1959 to 0/day in March 1960 implies mortality in the winter months. In early May 1960 the relative proportions of immature and spent individuals in the population was in the ratio 78 : 22%, and in February 1961 69 : 31%. The 1961 figures are shown in table 14.

TABLE 14. Condition of the ovaries in P. madidus in February, 1961.

Condition	No. dissected	%
Immature	9	69
Mature	0	0
Spent	4	31
Total	13	

In both cases this is an inversion of the ratio of autumn 1960. Callows were not observed until June and therefore it is concluded that the majority of the females forming the May peak had overwintered from the previous season. The spring reversal of the immature/spent ratio suggests that most of the winter mortality fell on spent individuals which had laid eggs in July and August, while immature females survived to lay early in the summer following emergence.

The proportion of mature females rose rapidly in June, falling slightly in July, and rising again in August before declining to zero in the autumn. This June-July peak was followed a month later by an increase in

the proportion in which eggs have been laid; this also fell slightly before rising to a maximum in the autumn. This is in agreement with early oviposition by females surviving the winter, in that there is in June and early July a trend towards the parous state due to egg-laying by overwintering females which was temporarily reversed later in July and in early August as the new generation of immature females emerged. In addition the mean ovary length reached a peak in June-July falling as eggs were laid, and rising in July-August as the emergent generation matured.

These observations confirm the suggestion that females emerging late in the summer overwinter as adults and breed early in the following season. No male reproductive organs were examined as no significant number of males appear to overwinter; there is a single peak of numbers and activity and it is concluded that the cycle is far simpler than in the female where at any one time a sample will show gonads covering a wide range of maturity.

Comparative notes.

This life-history is similar to that of Abax parallelopipedus, a close ally, described by van der Drift (1951), and summarised in the following section, although in Abax there appears to be more adult overwintering. In Pterostichus niger and P. melanarius whose annual cycles are not so well known as that of Abax, the life histories, as described below, are substantially the same as that of P. madidus with a single summer maximum and overwintering larvae.

This account of the life history of P. madidus is in agreement with that of Tipton (1960). Although in the latter work few gonad dissections were made fully mature males were recorded in late April, suggesting that

males became sexually mature sooner than the females, thus permitting the earliest individuals of a new generation to fertilise female survivors from the previous season.

c) Other species.

These accounts are based on the pitfall catches already described and are shown in figure 12 and Appendix tables 8-15.

In those species marked* the life histories are briefly described in unpublished work by Tipton (1960). In all cases these accounts agree with those at Silwood.

*Carabus violaceus. Adults were trapped from June to September with a maximum in July, the earliest capture being in May. Larvae were abundant in traps in late September and October. This agrees with van der Drift's (1951) account in Holland; here the first few adults to appear in the early summer are females which have survived the winter, followed by the males. Later in the summer comes major emergence of the generation which hibernated as larvae; breeding takes place in the autumn.

C. problematicus. Adults occurred from April to November with a peak in September and rather low catches in July and August; larvae were recorded in April. This is a predominantly larval overwintering species, although hibernating adults have been found at Silwood and elsewhere. Again, the life history has been described by van der Drift: adults emerge in May and June, aestivate during the following two months and reappear to breed in the autumn. In South Sweden Lindroth (1945) records a single adult peak in July.

Van der Drift points out that the July-August aestivation coincides with the maximum activity of Carabus violaceus, and suggests that this is a device by which the two species avoid competition; however the larvae of both species must occur together throughout the winter months.

C. nemoralis. Only small numbers of adults were trapped but they occurred from February until November with a main peak in May and a subsidiary one in October. Larvae were taken in June. Van der Drift records two adult maxima while in Sweden Lindroth's figures show a main peak in June, numbers falling in July with a slight increase in August. Delkerskamp (1930) describes a cycle in Germany in which reproduction takes place in the spring followed by May-July adult aestivation with some autumn activity; young imagines appear from July onwards and may be mated in the autumn. Hikimiuk (1948) gives a similar account of the biology of this species near Moscow where the active population of newly emerged adults in the autumn averaged only 70%,over four years, of the spring breeding population.

*Cychrus rostroides. Adults occurred at Silwood from June to September; no larvae were found. According to Lindroth this species overwinters as the larva, adults emerging in the summer.

Leistus ferrugineus. The majority of catches of this species were made in the autumn from late August into December, although some adults, many of them callows, were trapped in May and June. Larvae were taken in January and February. The life history appears to be similar to that of Nebria with a late spring adult emergence, summer diapause, a main period of breeding in the autumn and larval overwintering. Lindroth (1945) found a single June

maximum in Sweden while in Denmark Larsson (1939) recorded two peaks, one in June and one in September.

*Notiophilus biguttatus. Adults were most frequent in traps from April to early August with a peak in May and June; they were also taken in January and February, and a number were caught in September and October. Larvae occurred in the summer months, and in the collection of Silwood larvae were distributed: May - 1, June - 1, July - 7, August - 6, September - 1.

Overwintering is in the adult state with breeding in the summer months; the minor peak of catches in the autumn is therefore due to the generation of newly emerged adults. This agrees with Lindroth's account of the life history

*N. rufipes. The life history is the same as that of N. biguttatus, there being early summer and autumn peaks of adult activity. Although no larve have been found at Silwood low catches of adults in August and September suggest that this is the larval period. Similarly captures in February imply that N. rufipes is an adult overwintering species. This again agrees with Lindroth (1945) and Davies (1959), and Williams (1959) records it as breeding in the summer months.

At Silwood in 1959 and 1960 the late summer disappearance of the adults occurred a month later in N. rufipes than in N. biguttatus; this is probably not a real difference as in Scandinavia Lindroth records a June adult maximum in N. biguttatus and Larsson a May maximum for N. rufipes.

N. substriatus. Although catches of adults were low they suggest a life history similar to the two above. There were no captures between July and

September; the maximum occurred in June and there was some activity as early as February and as late as November. Of a series of eight specimens collected at Silwood three were taken in March, one in June and four in October. No larvae were found.

The cycle of this species is not described by Lindroth, but Larsson (1939) and Davies (1959) record it as overwintering as the larva, while it was considered by Williams (1959) to be a summer-larva species. The present observations tend to support the latter, although numbers are very small. Tischler (1955a) mentions that some small diurnal Carabid species are bivoltine and N. substriatus may be one of these.

* Loricera pilicornis. Adults were trapped from February to August with a maximum in April and May. Larvae are recorded in June and July. Lindroth found an adult maximum in June and that breeding occurred in the summer with the adults overwintering. In Central Germany Geiler (1960) recorded maximum pitfall catches from May to July. At Silwood larvae have been recorded in the early summer from May to July.

Bembidion lampros was trapped from February to October, the maximum numbers being taken in the period May to July. Overwintering adults were found but no larvae. According to Lindroth it overwinters as the adult with summer larvae. He recorded an adult maximum in Sweden in June.

* Harpalus rufipes. Adults were trapped from March to October, with large numbers from June to August when callows were common; larvae were recorded from August to November. Briggs (1957) has described the life history of this species in some detail. Eggs are laid from mid-July until late September, the resulting larvae overwintering and producing callow adults in the summer.

Some adults emerge in the autumn and may not breed until the following season.

H. affinis. Adults were taken in pitfalls from April until November with a maximum between May and August, when callows were frequent. Larvae which can almost certainly be assigned to this species occurred from June to October. According to Briggs (1957) the life history is similar to that of H. rufipes.

Amara communis was trapped from March to July with a peak in late May and early June; callows were active in September. Large numbers of Amara larvae have been taken but it is not possible to determine their identity further than the sub-genus. Lindroth considers this an adult overwintering species with a summer larval period, and this evidently applies at Silwood. In Sweden, however, a single peak in May and June is described with no autumn increase in activity.

A. lunicollis. The life history is very similar to that of A. communis; the main period of adult activity is in July, numbers in traps are low in August and callows have been taken in September. Again this is an adult overwintering species differing from A. communis only in having an adult maximum later by approximately one month.

*Stomis pumicatus. Adults were trapped from April until July, the greatest numbers occurring in May and June; occasional catches were made in September. No larvae or callows were found. According to Larsson it overwinters as the adult, breeding early in the year and therefore autumn catches are probably of newly emerged adults.

*Pterostichus caerulescens was present in traps from February to November, the greatest numbers occurring between May and July, when copulation was recorded. Callows occurred and there was a second peak of catches in autumn, which in 1960 exceeded the earlier maximum. No larvae were taken but overwintering adults have been found. From this it would appear that the larval period lasts from May-June until August-September. Lindroth recorded a single summer maximum in Sweden with a slight increase in numbers in August which may represent adult emergence.

*P. niger was trapped from April until October with a maximum in August during which copulation was observed. No larvae or callows were found at Silwood but overwintering adults of both sexes have been recorded. Van der Drift mentions callows in July in Holland, while Lindroth records a June adult maximum in Sweden. In Denmark, Larsson obtained larvae throughout the year, most commonly in November, and an August adult maximum with callows in June and July. These observations suggest autumn breeding and mainly winter larvae, although from the extent of adult overwintering in Britain and Larsson's larval records it seems that either individuals may breed in two seasons, or those emerging late in one season do not breed until the next.

*P. melanarius. This species was trapped between February and October, being commonest between June and August; larvae were recorded in January and October. The life history is described by Briggs (1957): the eggs are laid in August and September, and larvae are present until April. (Lindroth (1956b) records obligatory winter diapause in the second instar

larvae). Pupae may be found in May and the new generation of imagines appears in June; there is some adult overwintering.

Abax parallelopipedus. Active adults first appeared in March, becoming abundant in May after which catches fluctuated about the same level, apart from a slight increase in July and early August; at the end of August numbers declined rapidly although occasional individuals were trapped up to mid-November. Copulation was frequent during the summer maximum. Overwintering adults of both sexes were found at Silwood under logs and in litter.

Changes in the sex ratio in traps for 1960 are shown in table 15.

TABLE 15. Abax in traps 1960: % ♂

Month	M		J		J		A		S		O	
Period	6	7	8	9	10	11	12	13	14	15	16	17
No. of Abax examined	61	62	75	68	127	151	105	98	45	11	5	12
No. ♂	36	35	42	39	75	92	60	44	22	4	2	4
% ♂	59	56	56	57	59	61	57	45	49	36	40	33

No callows were seen. Larvae occurred throughout the year, being most abundant in traps in September and October.

The life history has been investigated by van der Drift. In his account adults were first active in early May with no initial dominance of

female activity. This agrees with table 15 above and is in contrast with P. madidus. Eggs are laid in the summer and autumn, and the presence of females with mature ovaries in May led van der Drift to conclude that some emerge in the autumn and do not lay eggs until the following season; thus old females reproduce in the spring and summer, and young in the summer and autumn. He recorded larvae from October until May.

At Silwood a high percentage of males in traps in May, and recorded male overwintering suggest that in this species, unlike P. madidus, it is not only in late emerging females that reproduction may be delayed until the following season.

* Calathus fuscipes. Adults were most commonly trapped in the late summer and autumn from July to October although occasional specimens were taken throughout the year. No callows or larvae were recorded. The life history is described in N. Wales by Gilbert (1956); the species showed maximum activity in July and August disappearing in October and November. Eggs were laid from July to October and larvae overwintered in the final instar. Some adults survived into a second season in which they may have reproduced.

* C. melanocephalus adults occurred at the same time as those of C. fuscipes and the annual cycles are similar; no callows or larvae were found. Gilbert records differences between the two species. In N. Wales C. melanocephalus showed an adult maximum later than that of C. fuscipes in September and October; egg-laying lasted from July to October and all three larval instars occurred during the winter. Lindroth (1945) cites this species as overwintering as the adult in eastern Finland.

* Calathus piceus Adults were trapped from April until December and in large numbers from May to the end of August with a maximum just before the autumn decline. No larvae or callows were found. According to Larsson it is a larval overwintering species in Denmark.

Synuchus nivalis. In July 1959 this species was abundant in traps although in 1960 only two individuals were found. A larva was taken (25/10/60) which may belong to this species. Lindroth (1956a) has described the life history in Sweden where it shows a July adult maximum, overwintering as the larva.

Agonum dorsale. occurred in traps from March to October with a maximum in May and another smaller one in the autumn; adults were found under stones and logs in the winter months. Callows occurred in August and September. Dicker (1951) has recorded oviposition by th s species on the under-side of strawberry leaves from May to July; ova required 7-10 days incubation, and in one observation the imago emerged exactly four weeks after the hatching of the larva. This is therefore an adult overwintering species and a summer breeder. Lindroth's figures for S. Sweden show a June maximum and a slight increase in numbers in September. Geiler (1960) recorded July maxima in traps in central Germany.

d) Classification of life history types.

Lindroth (1945) divided Carabidae according to their life-histories into two groups, those with overwintering adults, and those with overwintering larvae, while Larsson (1939) described them respectively as spring and

autumn breeding. At Silwood some larval overwintering species show spring and autumn peaks of adult activity, and in a number of adult overwintering species there may be autumn activity by newly emerged adults. Therefore a further division of Carabid life histories is possible on the basis of whether there are one or two annual maxima of adult activity. Species falling into each of the four classes are shown in table 16.

In fact active individuals of the majority of spring breeding species do occur in the autumn, but only in the two species shown in the table are they at all numerous relative to the period of breeding activity. This scheme is also slightly complicated by extensive adult overwintering in autumn breeding species which leads to extended breeding seasons.

Lindroth (1945) observed that a high proportion of larval overwintering Carabid species is typical of an Atlantic climate, and that in Continental areas larval overwintering species may overwinter exclusively as adults, for example Calathus melanocephalus.

In figure ~~13~~ 12a the pitfall catch histograms in figures 8-10 and 12 are diagrammatically summarised. This shows the periods during which more than occasional individuals of each species were trapped, and the month of maximum activity; except for Nebria the immediate post emergence captures of such species as L. ferrugineus and P. caerulescens are not shown.

TABLE 16. Types of Life History in Silwood Carabidae.

Overwintering stage	Single maximum	Two Maxima
Adult	*Loricera*	*C. nemoralis*
	Agonum dorsale	*P. caerulescens*
	Amara communis	
	A. lunicollis	
	B. lampros	
	N. biguttatus	
	N. rufipes	
	N. substriatus (?)	
Larva	*H. rufipes*	*N. brevicollis*
	H. affinis	*C. problematicus*
	C. violaceus	*L. ferrugineus*
	Synuchus	
	P. melanarius	
	P. niger	
	P. madidus	
	Abax	
	C. piceus	
	Cychrus	
	C. fuscipes	
	C. melanocephalus	

From the distribution of the adult maxima three distinct seasonal facies may be distinguished:

I. March-June

Loricera
Agonum dorsale
C. nemoralis
Amara communis
Notiophilus spp. (3)
Stomis
Nebria (spring emergence)
B. lampros
P. caerulescens

II. July and August

A. lunicollis
H. rufipes
H. affinis
C. violaceus
Synuchus
P. melanarius
Calathus piceus
Abax
P. niger
Cychrus
P. madidus

III. September and October

Calathus fuscipes
C. melanocephalus
Carabus problematicus
Nebria (autumn breeding season).
L. ferrugineus

The more abundant species, especially N. brevicollis and P. madidus, tend to be trapped throughout the year, and conversely the occurrence of less common species shows more restriction to limited periods; therefore the latter may be most conveniently used to define the three facies.

The period March to June is characterised by the trapping of Stomis and Amara communis, and newly emerged Nebria are abundant. As A. communis declines A. lunicollis appears in numbers and defines the beginning of the next facies lasting through July and August. This can be rather narrowly described by the maximum activity of Carabus violaceus, Cychrus and Synuchus, and also by the peak activity of P. madidus. As mature A. lunicollis disappear from traps in late August there is a rise in the catches of Calathus fuscipes and C. melanocephalus, indicating the replacement of the summer by the autumn facies. Typical of the latter are breeding Nebria and L. ferrugineus.

The true maxima of spring facies species occur from late April until June, and extension of this period back to the beginning of March is due to the fact that the majority of the spring species overwinter as adults, and may appear in numbers, presumably as temperature permits, from the end of February onwards.

During November and December the only adult Carabidae commonly trapped are either survivors of the summer and autumn facies, P. madidus, Nebria, L. ferrugineus, and the two autumn Calathus species, and newly emerged summer-larvae species, P. caerulescens and Notiophilus species; of these nine Carabidae five (55%) overwinter as larvae. In January and February Nebria and P. madidus still occur, with the adult overwintering species

Loricera, C. nemoralis, Notiophilus species, B. lampros and P. caerulescens; of these, two of nine species (22%) overwinter as larvae.

The percentage of larval overwintering species in each facies may be compared (Table 17).

TABLE 17.

	Facies	No. spp.	No. larval overwintering spp.	% total.
I	Spring	11	1	9
II	Summer	11	10	91
III	Autumn	5	5	100
	(Nov-Dec	9	5	55)
	(			)
	(Jan-Feb	9	2	22)

From November to February the species were selected by their relative abundance in traps within a given period, and the percentage figures are not comparable with those for March to October where species are placed in a facies, singly, when the whole year is considered. However, during the period March to October there is an obvious replacement of adult overwintering species which are active early in the spring, by larval overwintering species which, by the end of June, become the most numerous. In agreement with this the November to February figures do show a reversal of the trend with the autumn emergence of adults of spring-breeding species, which by January and February predominate.

3) DISCUSSION.

There is some evidence that the exact form of life history in Europe or the prevailing type, vary with latitude and longitude. In the direction North-South there is a trend towards a single annual maximum of adult activity in the North becoming divided into distinct spring and autumn peaks in the South. This may be related to the increased length of the summer in the South and the higher temperatures reached. The East-West trend is from a large proportion of larval overwintering species in the West to adult overwintering in the East (Lindroth 1945). Here the climatic difference lies in the transition from an atlantic climate with relatively mild winters to a continental one with a drier winter and greater difference between winter and summer temperatures.

It is possible that the larval overwintering habit in atlantic Europe leads, as weather permits, to a certain amount of winter feeding and development, as in Nebria brevicollis (Williams 1959), which in a continental climate is precluded by low temperatures. Similarly in the latter areas winters are drier and there is a possible advantage in the more desiccation-resistant adults enduring them.

The single peak of adult activity in such spring breeding species as C. nemoralis, and P. caerulescens in Sweden, contrasting with the widely spaced double peaks in Britain is probably a direct effect of the shorter Scandinavian summer, in which low temperatures may extend the larval period, and the earlier onset of winter conditions reduce activity in newly emerged adults.

However, the presence of a summer diapause in three of the larval overwintering species is not so easily rationalised. The case of Nebria will be discussed.

There is evidence that dormant arthropods show greater ability to withstand desiccation than active stages (Birch and Andrewartha 1942), but Lees (1955) has suggested that diapause should be regarded primarily as a timing mechanism to regulate the life cycle, either to synchronise adult emergence, or as Andrewartha (1952) has emphasised, to ensure that active stages are present when food supplies or physical conditions are suitable. The diapause in N. brevicollis may be examined as a stage resistant to unfavourable conditions and as a timing device.

The first suggestion, although initially attractive, is unlikely to be important in Nebria. The unimodal curve of adult activity in Scandinavia which is separated into two distinct peaks in the longer summer of Britian, in conjunction with the species' woodland habitat and humidity tolerance and preference (Tipton, 1960), implies that the July-August diapause is a device to overcome the low humidities usually associated with high temperatures. However, the 30 year averages of rainfall, temperature and humidity at Kew give no support to this (table 18). July and August show both higher temperatures and rainfall than either June or September with the result that there is no fall in humidity during the hotter months.

Similarly the larval overwintering species with a summer diapause showed a significantly greater fall in catch in 1960 than species with other types of life history (Appendix 4). Again this does not support

the suggestion that the diapause aids adult resistance to the effects of an unfavourable summer.

TABLE 18. 30 year averages (1921-51) at Kew Observatory.

Month	Mean Temp. °F.	Rainfall mm.	Relative humidity % hrs. G.M.T. 0700	1300	1800
June	60	48	78	57	59
July	64	62	80	57	59
August	62	57	85	61	63
September	60	50	90	64	72

There remains a possibility that the summer diapause may delay breeding until the autumn when some environmental factor, perhaps humidity, becomes suitable for the larvae. Alternatively, Lees (1955) cites a number of cases in phytophagous arthropods where diapause is governed by physical factors similar to those which limit growth of the food plant, guaranteeing some correlation between the development of the animal and its food supply. Nebria however is a catholic predator on a variety of Collembola species and other arthropods inhabiting litter (Davies 1959) and it is difficult to relate diapause to the feeding requirements of general predators; although Evans (1955) described spring and autumn peaks, coinciding with those of N. brevicollis, in the numbers of Acarina and Collembola in litter and soil under Spruce.

There are other cases however in which diapause appears to regulate adult emergence with the effect of synchronising breeding activity in a population. Lindroth (1956) has pointed out that should the breeding

activity of all or part of a population become out of phase with the normal seasonal cycle there is an increased probability of its members being wiped out by unfourable climatic conditions. An example of such a diapause is that described by Corbet (1954) in Anax imperator (Odonata), and the autumn and winter diapause in the second larval instar of Pterostichus melanarius may be another. In the latter Lindroth found that all individuals entered the diapause whatever the conditions of the external environment. Thus larvae which may have hatched over a considerable period in the summer all enter the winter at the same stage; during the winter months low temperatures will inhibit development, and this will be resumed in the spring by a larval population all of whose members are in the same instar. They can then be expected to reach maturity and emerge at roughly the same time.

Davies (1955) and Williams (1959) have suggested that in Nebria breeding may extend throughout the winter; the maximum numbers of first instar larvae were recorded in mid-November both by Williams and in the present work, and the peak of spring emergence occurs approximately six months later. First instar larvae are found until the beginning of April and at summer temperatures they may be expected to reach the adult state at least a month before the onset of the main breeding activity. Thus in this case and possibly also in C. problematicus and L. ferrugineus the summer period of adult diapause may ensure that all individuals reach a similar state of sexual maturity by the beginning of the breeding season thus preventing the establishment of two genetically isolated elements of the same spatial population.

B. II. HABITATS OF CARABIDAE AT SILWOOD.

1) Vegetation of Field Station.

Silwood Park lies on Eocene sands of the Bagshot and Bracklesham beds and in places these are overlain by Thames Terrace gravels. The resulting soil is sandy and frequently contains a high proportion of waterworn pebbles, as for example on Wood Bank and in an arc from South Lodge Wood across North and South Gravels to Observatory Copse. In such soils Carbonates are absent or present in negligible quanities (Hall and Russell 1911) and pH is low, although at Silwood podsolisation is slight.

From the head of the Marsh, around the lake to Nash's Copse the sandy soil is overlain by peat, but this coincides with the wetter, lower-lying part of the Field Station whose Carabidae are not dealt with in this study and its vegetation will not be discussed. Over the remainder of the area the "natural"vegetation can be divided into three basic types, grass heath, oakwood and beech wood.

The grass heath is dominated by the grasses:

Agrostis tenuis Sibth.

Anthoxanthum odoratum L.

Dactylis glomerata L.

Deschampsia flexuosa L.

Festuca rubra L.

Holcus mollis L.

Poa pratensis L.

Of these D. glomerata is locally dominant and has been introduced.

Other common plant species are:

Luzula campestris L.

Achillea millefolium L.

Campanula rotundifolia L.

Cirsium arvensis L.

Cerastium arvensis L.

Galium hercynicum Weigel

Hieracium sp.

Plantago lanceolata L.

Ranunculus acris L.

Rumex acetosella L.

Veronica chamaedrys L.

In grassland in partial shade on the edge of wooded areas and below the canopies of isolated trees, Dactylis and Holcus become dominant, with nettles Urtica dioica L., and the umbellifer Conopodium majus Gowan.

The most important constituent of the oakwood is Quercus robur L., but other trees are common including Pinus sylvestris L., beech Fagus sylcatica L., and sweet chestnut Castanea sativa Mill.. The canopy is typically open as on Wood Bank and in Hell Wood and Nash's Copse, and below the trees birch Betula pubescens Ahrh. is frequent and Rhododendron ponticum L. occurs. The herb layer commonly consists of the heath grasses Agrostis, Deschampsia, Festuca and Holcus with bramble Rubus fruticosus agg., and abundant bracken Pteridium aquilinum L.; Calluna vulgaris L. is occasional.

In the beechwood a characteristic closed canopy produces dense shade and a floor of bare litter; but in some areas especially Garden, Heath

and South Lodge Woods, Rhododendron is abundant. The grasses Agrostis, Anthoxanthum, Deschampsia and Poa occasionally occur as light intensity permits, and bracken may invade the edge of the beechwood.

This division of the Silwood vegetation is complicated by three factors:

1. Present land use.
2. The history of the Field Station.
3. The relations between the basic vegetation types.

1. This mainly affects potential heath areas, which are in practice pasture or arable land, and in the latter case waste areas support a flora very different from the true heath, characterised by ruderals, especially Chenopodiaceae, Polygonaceae, and ephemeral grasses. This pioneer vegetation found around the edges of cultivated areas possesses a distinctive Carabid fauna which may be a reflection of the plant species present or of cultural practice. That such land will revert to heath if neglected is shown by parts of Pond Field, which were cultivated in 1958 but throughout the summer of 1959 received no attention and by September 1959 were covered by heath grasses.

2. The Field Station was once a deer park, hence much of the woodland and all the isolated trees are 'unnatural' in that they are the result of planting or the planned thinning of older woodland. It is probable that Quercus petraea L. would naturally occur on the siliceous soil of Silwood Park, but Jones (1959) mentions that by the end of the eighteenth century Q. robur was the only species planted and this may explain its predominance at Silwood.

The original ornamental function of parts of the area also explains the presence of the once alien but now, on sandy soils, completely naturalised Rhododendron.

A feature of the Field Station is a vigorous growth of scrub consisting of young oak, birch, beech, holly, Ilex aequifolium L. and hawthorn Cratageus oxycanthoides Thuill. with some rowan Sorbus ancuparia L while below and beyond these bracken and bramble are abundant. Such scrub can be seen on Elm Slope, Hell Hill and Pound Hill and in parts of Nash's Copse and Man's Copse and on the edge of Lake Wood. A large part of this scrub growth can be attributed to the absence of grazing by deer, present until some 15 years ago, with the more recent disappearance of rabbits contributing.

3. The plant communities of siliceous soils in S.E. England are described by Tansley (1953) and among them the vegetation types referred to above, and their seral relationships are discussed, although these are not properly understood. In particular the status of the oakwood is uncertain.

Tansley has described a simple succession from grass heath through birch scrub to mixed oakwood (Q. robur with Q. petraea), when grazing is absent, the latter subsequently being replaced by beech. And to some extent this series can be seen at Silwood although very much obscured by scrub of Rubus, Betula and Crataegus, with Pteridium. However, scrub of this kind has been described by Adamson (1932) as a stage in the development of Quercetum petraeae as a climax from cleared woodland and ungrazed common-land (again suggesting that Q. petraea may be the natural

Silwood species). The initial establishment of such scrub protects seedling oaks from any subsequent grazing and on the Field Station it can be interpreted as an early stage in the spread of oak. Thus oakwood may follow birch or mixed scrub, although at Silwood mature oakwood is typically open which permits a dense growth of Betula and Pteridium, and this occurs even in degenerating woodland so the presence of scrub does not necessarily imply the spread of oak.

The oakwood is further complicated by the presence of beech and pine, the former occasionally dominant in small areas, leading Tansley to call a similar community 'Beech - oak - pine - birch - heath'. However, pine is usually associated with podsolisation which is slight at Silwood, but nearby in Windsor Great Park and at Wentworth where the soil is similar but in places shows a more developed podsol, Pinus is locally dominant; it usually occurs with Calluna heath which again is not common at Silwood.

Tansley suggests that beech is impermanent on acid sandy soils, but at Silwood it shows signs of regeneration; both oak and beech saplings occur among scrub, and Watt (1934) has shown that on acid loam soils where oak and beech are in competition the former usually becomes dominant. Thus in the Silwood area pure stands of beech may regenerate but they are relatively scarce, and perhaps one may conclude that its advantage over oak on acid siliceous soils is slight. Were this not so far larger areas dominated by beech might be expected.

The relationships between the various types of vegetation discussed may be represented in diagrammatic form (figure 13). This indicates the importance of the grazing factor in permitting the regeneration of

woodland, and the establishment of the initial stages. The occurrence of either birch or Rubus-Crataegus scrub would seem to depend partly on soil acidity and partly on the proximity of parent plants.

At Silwood grass heath and beechwood are distinct but it appears impossible to separate the intermediate stages which occur as a mosaic together with occasional areas of heath grasses and isolated beech trees, and comprise the oakwood. The only other vegetation type which is distinct is Pteridetum which occurs at all stages in the succession and is little affected by grazing or podsolisation.

2) Distribution of Carabid species.

a) Introduction.

To demonstrate the habitats of some of the more abundant Silwood Carabidae the catches of traps in various types of vegetation may be compared. Four such habitats are considered:

1. Pteridetum - the ground covered with oak or beech leaves.
2. The litter covered floor of beechwood.
3. Grass heath.
4. 'Arable land' - the bare of weed-covered ground between experimental plots or crops.

All these types have the advantage of being rather uniform in any one place and presenting very similar physical and vegetational characters at different points on the Field Station. The Carabid fauna occurring in oakwood has not been investigated owing to problems resulting from the patchy dominance of different tree, shrub and herb species.

23 traps in various types of vegetation were visited regularly from mid-October 1958 to the end of November 1959 and from the beginning of March to the end of November 1960 and the distribution of species in them broadly indicates the habitats of the commoner Silwood Carabidae. These observations are supplemented by the catch of the following traps:

Two transects across the border of woodland and grass heath.

One short transect in woodland.

A number of traps on arable land.

Comparison of catches of a plot in beech litter and a similar one in grassland.

As far as possible records were kept of the habitats of all Carabidae, both larvae and adults, observed on the Field Station between October 1958 and autumn 1960.

In Section A III of this thesis it was argued that pitfall traps should be used only with considerable discretion to contrast the relative number of a species in several different habitats. Here only large differences are considered significant. In the case of four common species the habitats as indicated by the results below are misleading and general experience shows them to be widely distributed at Silwood. They are:

Carabus violaceus

Loricera pilicornis

Notiophilus substriatus.

Synuchus nivalis.

b) Occurrence of adults in pitfall traps.

The 23 traps operated between 6/10/58 and 24/8/59, and 2/3/60 and 30/11/60 can be divided into three groups according to the type of vegetation in which they were situated.

1. Pteridetum. 3 traps on Wood Bank.
2. Beech litter. 8 traps in Garden and Heath Woods, and on Wood Bank.
3. Grass heath. 9 traps in Silwood and Hill Bottoms from Elm Hill to Pond Field.

The remaining three traps will be considered individually: one in Hill Copse, one on the edge of the Heath, and the last on Elm Hill.

Results from the 20 traps are shown in table 19. This suggests

that the Carabidae taken can be divided into three main groups; species of woodland, those of grassland, and species commonly occurring in both habitats.

Here the woodland species can be further divided into those restricted to, or most abundant in, bracken: Stomis, Leistus ferrugineus, Abax, and C. problematicus; and those commonest under beech: Cychrus, Calathus piceus, Notiophilus rufipes and Nebria brevicollis. However, at Silwood bracken usually occurs on the edge of beechwood and among scattered oaks, and the true beechwood species occur both in it and in leaf litter of other tree species. The only species found almost exclusively in beech litter is Notiophilus rufipes, but even this has also been taken in oak, elm and horse-chestnut litter with no beech nearby. Similarly, the bracken species seem to be not so much typical of bracken, but of moderate woodland conditions, that is those that apply at the edge of canopied areas, rather than in the densely shaded interior.

The three large Pterostichus species, P. niger, P. madidus and P. melanarius occurred in all the habitats here considered, although P. madidus appears to be slightly more common in grassland, and P. melanarius more obviously so, as is indicated by the arable land traps (Tables 20 and 21 Other species frequently found in all habitats are the four mentioned above, C. violaceus, Loricera, N. substriatus and Synuchus.

Like the woodland species the grassland Carabidae also form a distinct group, characterised by Carabus nemoralis, Calathus fuscipes and C. melanocephalus, the common Amara species, Pterostichus caerulescens, Bembidion lampros, Harpalus rufipes and H. affinis. Here again further

TABLE 19. Distribution of Carabidae in 20 traps October 1958 - November 1960.

	Species	Vegetation and no. of traps. Beech litter (8)	Bracken (3)	Grass heath (9)	Mean No. Carabidae/ trap. Beech litter	Bracken	Grass heath
(a)	N. rufipes	12			1.5		
	C. piceus	192	10	1	24.0	3.3	0.1
	N. brevicollis	2668	180	134	335.5	60.0	14.9
	C. rostroides	7	2		0.9	0.7	
	N. biguttatus	22	5	5	2.7	1.7	0.6
(b)	A. parallelopipedus	161	127	21	20.1	42.3	2.3
	C. problematicus	3	7	2	0.4	2.3	0.2
	L. ferrugineus	3	10		0.4	3.3	
	S. pumicatus	1	27		0.1	9.0	
	C. nemoralis		1	7		0.3	0.8
	A. communis			27			3.0
	A. lunicollis			78			8.8
	C. fuscipes			75			8.3
	C. melanocephalus			34			3.8
	P. caerulescens		1	54		0.3	6.0
	H. rufipes	2		105	0.2		11.7
	H. affinis			13			1.4
	B. lampros			22			2.4
	A. dorsale			4		0.4	
	P. melanarius	1	2	22	0.1	0.7	2.4
(c)	P. niger	13	8	21	1.6	2.7	2.2
	P. madidus	771	64	982	88.9	21.3	109.1
	N. substriatus	2		2	0.2		0.2
	S. nivalis	6		3	0.7		0.3
	L. pilicornis	6			0.7		
	C. violaceus	60	9	12	7.5	3.0	1.3

(a) Woodland species.

(b) Grassland species.

(c) Widely distributed species.

division into two groups is possible; the grass heath species and those found on arable land. This is shown by the catch of traps on cultivated ground in Hill Bottom, two between the beginning of May and the end of August 1959, and three, visited rather irregularly between the beginning of May and the end of November 1960 (tables 20 and 21).

In them some of the grassland species appeared to be particularly abundant: Bembidion lampros, Harpalus rufipes and H. affinis, Pterostichus melanarius and Agonum dorsale. Less common than on grass heath were Amara communis, A. lunicollis and P. madidus. Bare or sparsely weed-covered soil presents less of an obstacle to Carabid movement than the grass heath and where arable land catches are lower than those of the heath they must indicate a real difference in population. Also very common on cultivated land, but less abundant on grass heath were a number of diurnal Amara and Bembidion species but these were not easily taken in pitfalls (see Section A III 2).

The presence of the woodland species Nebria brevicollis, Notiophilus biguttatus and Stomis, in the Hill Bottom traps can be attributed to the proximity of Hill Copse.

Scherney (1955, 1960), Abu Yaman (1959) and Geiler (1960), gave very similar lists (and relative numbers taken in traps), for arable land in Holland and Germany.

The catches of the other three traps may be related to this division of the Carabidae into 5 groups. The Heath trap (table 22) was situated in scrub of Hawthorn and Quercus cerris L. between beechwood and grass heath. It was not a productive trap but shows a woodland fauna with very few

TABLE 20. Catch of Carabidae in two traps on arable land in Hill Bottom. May - August 1959.

Species	Total for 2 traps	Mean/trap
Nebria brevicollis	9	4.5
Stomis pumicatus	1	0.5
Amara communis	1	0.5
Calathus fuscipes	7	3.5
Pterostichus caerulescens	11	5.5
Harpalus rufipes	115	57.5
H. affinis	42	21.0
Bembidion lampros	70	35.0
P. melanarius	53	26.5
Pterostichus niger	1	0.5
P. madidus	59	24.5
Loricera pilicornis	1	0.5

TABLE 21. Catch of Carabidae in 3 traps on arable land in Hill Bottom. May - November 1960.

Species	Total for 3 traps	Mean/trap
N. brevicollis	19	6.3
N. biguttatus	1	0.3
C. nemoralis	1	0.3
A. communis	2	0.7
A. lunicollis	1	0.3
C. fuscipes	47	15.3
C. melanocephalus	9	3.0
P. caerulescens	17	5.7
H. rufipes	68	22.7
H. affinis	65	21.7
B. lampros	88	29.3
P. melanarius	17	5.7
A. dorsale	21	7.0
P. madidus	17	5.7
N. substriatus	3	1.0
L. pilicornis	2	0.7
C. violaceus	2	0.7

TABLE 22. Carabidae taken in 3 of 23 traps.

1) In litter on edge of heath.
2) Under sycamore on Elm Hill.
3) In Hill Copse.

	1	2	3
N. rufipes		3	2
C. piceus	1	109	10
N. brevicollis	20	141	157
N. biguttatus		3	1
A. parallelopipedus	48	71	7
C. problematicus		2	1
L. ferrigineus		1	4
S. pumicatus		1	1
C. nemoralis		1	
A. communis	1	1	
C. fuscipes		2	
P. caerulescens			2
H. rufipes		2	
H. affinis		1	
B. lampros			1
P. melanarius			2
P. niger	2	7	3
P. madidus	105	127	146
L. pilicornis	1	5	
C. violaceus	6	1	3

grassland species occurring; the rather high catch of Abax and the low numbers of Calathus piceus and Nebria brevicollis do not suggest extreme woodland conditions.

The trap on Elm Hill (table 22) was in intense shade under sycamore with beechwood on one side and grass heath within a few yards on the other and along the woodland heath boundary was a vigorous growth of elm scrub. Thus this trap took bracken or 'edge of wood' species - Stomis, Leistus ferrugineus, Abax and Carabus problematicus, true woodland species - Notiophilus rufipes, Calathus piceus and a high catch of Nebria brevicollis, and also a few grass heath species - Calathus fuscipes, Amara communis, Harpalus rufipes and Carabus nemoralis.

Hill copse consists of scattered oak, elm (Ulmus procera Salisbury) and beech, with a ground layer dominated by Holcus mollis. As in the Elm Hill traps the Carabid fauna (table 22) shows true woodland forms, Notiophilus rufipes and Calathus piceus, and less extreme elements, Stomis, Leistus ferrugineus and Carabus problematicus; again grassland species occu Pterostichus caerulescens, Bembidion lampros and Calathus melanocephalus.

Two transects of traps were laid out on Elm Hill as shown in figures 14 and 15.

Transect 1. consisted of a line of 13 traps at intervals of 6 yards:

trap 1) In grass heath near its junction with a mown area, and just below the canopy of a lime (Tilia).

2 - 9) In grass heath.

10) In Holcus and Dactylis with Conopodium, on the edge of woodland.

11 - 13) In sparse Holcus below beech canopy.

The traps were visited between 13/5/59 and 24/7/59. The results are shown in Appendix table 16 and figure 14.

Transect 2). Of 11 traps spaced at 5 yds. was visited from 27/5/59 to 25/11/59, and 2/3/60 to 30/11/60.

trap 1) In sparse Holcus under beech.

2 - 3) In beech litter.

4 - 6) In Holcus under beech.

7 - 9) In Holcus and Dactylis with nettles, shaded by beech.

10 - 11) In grass heath.

Tables for the two seasons are combined and shown in Appendix table 17 and figure 15.

These transects illustrate the transition from a grassland Carabid fauna to a woodland one under beech canopy, although most of the woodland floor involved here is not typical of either the bracken or beech litter types mentioned previously. However, although the distributions of the species belonging to the various habitat types tend to overlap, the results do confirm earlier conclusions. Such woodland species as Notiophilus rufipes and N. biguttatus, Nebria brevicollis and Calathus piceus are largely restricted to areas below the canopy, the last two species being most abundant in transect 2) in the traps in the beech litter. Abax was the most frequent bracken or 'edge of wood' species and spread some way into grass heath; transect 2) demonstrates maximum captures in the zone between litter and grass heath. In both transects grassland species (for example Amara species, B. lampros and P. caerulescens) are more closely confined to their typical habitat. However, there are anomalies especially

in the distribution of Nebria. In transect 1) the highest catch was made in the heath, although this probably represented a population centred on the litter-covered area below the lime tree, where collections from March to June 1960 yielded both second and third instar larvae and callow adults. The relatively high catch of Nebria in the heath traps (10 and 11) in transect 2) is less easily explained. One of the traps visited daily from 1958 onwards was situated in the grass heath 20 yards from these two traps and took adults, callows and larvae. This indicates the presence of a breeding population, and may be related to the fact that this part of the heath is relatively well shaded during most of the day, with Elm Hill woodland lying only 20-30 yards to the South-west.

A third transect in South Lodge Wood was visited on 15 occasions between 13/5/59 and 27/7/59. It consisted of 5 traps at 4 yard intervals on beech litter; trap 1) was in litter one yard from a dense clump of Rhododendron, and the centre of the transect was crossed by a track where a bare sandy soil suppoted a sparse growth of Poa pratensis. The relation between numbers per trap and depth of litter have been discussed in Section A III. The total catches of these traps are shown in table 23.

The majority of the Carabidae taken are widely distributed species, or typical of woodland, but in the centre of the transect in the area of the track Bembidion lampros S.S and Asaphidion flavipes occurred; the former is normally found only in grassland and along the edges of ploughed fields, and the Asaphidion has a similar distribution in sandy districts. Both are small species less than 4.5 mm. long, the Bembidion being flightless. They have not been taken elsewhere in beechwood, and the capture of these

small, grassland species in the middle of the transect must be attributed to the physical properties of the sandy substrate, or to some aspect of its fauna or flora, rather than to any increased mobility it permits. This suggests that discrete populations of some Carabid species can exist in very small and restricted areas.

A final comparison can be made between catches in two unenclosed plots 10 yards square, each of 10 traps, between 13/7/59 and 27/8/59. One was on litter below a closed canopy of beech in South Lodge Wood, with Rhododendron 15 yards away on three sides, while the other was on grass heath on Elm Hill with a copse of oak and beech 25 yards distant on one side. Catches are shown in table 24.

These catches show the difference between the Carabid fauna of beech litter and that of grass heath uncomplicated by the presence of 'bracken' or arable species. Trapping was only carried out over 6 weeks in late summer and many early and autumn species were absent or present in small numbers, for example Nebria brevicollis, Carabus nemoralis, and Amara species. Indeed the only abundant species was Pterostichus madidus, but woodland-grassland differences are evident. Only three species occur in both plots, the widespread Carabus violaceus and P. madidus, and Abax. The presence of the latter in the Elm Hill plot is almost undoubtedly due to the presence of the copse 25 yards from the plot, and transects 1) and 2) showed that the distribution of this species, although centred on woodland may extend some way into grass heath.

TABLE 23. Carabidae occurring in Transect 3. 1959.

Species \ Trap	1	2	3	4	5
Abax parallopipedus	5	4			
Cychrus rostroides			1		
Calathus piceus		2	2	5	
Notiophilus rufipes	1		1		
Nebria brevicollis	47	76	70	56	28
Pterostichus niger	1	11		1	
P. melanarius			1		
P. madidus	7	6	5	4	8
Bembidion lampros		3	3	2	
Asaphidion flavipes			1		
Carabus violaceus	3	2	2		
Loricera pilicornis		1	4	2	3
Notiophilus biguttatus	2	2	5	8	
N. substriatus			1		
Mean depth of litter (inches)	0.93	0.3	0.05	0.45	1.25

TABLE 24. Carabidae trapped in two plots of 10 traps between 13/7/59 and 28/8/59.

1) In beech litter in South Lodge Wood.

2) In grass heath on Elm Hill.

Species	Total Nos. trapped.	South Lodge Wood (Beech litter)	Elm Hill (Grass Heath)
Abax parallelopipedus		10	2
Cychrus rostroides		1	
Calathus piceus		23	
Nebria brevicollis		10	
Pterostichus niger		8	1
P. melanarius			1
P. madidus		344	254
Calathus fuscipes			11
C. melanocephalus			6
Pterostichus caerulescens			1
Harpalus rufipes			2
Carabus violaceus		8	4
Synuchus nivalis			4

c) Occurrence of larvae.

For approximately half the common species considered here larvae have been recorded at Silwood in numbers. They were taken in soil samples, traps and hand collections, and it is not practicable to assess their distribution quantitatively. They were identified from van Emden's (1942) key.

Carabus violaceus: Larvae were common both in beech litter and on grass heath; occasional individuals occurred on cultivated ground.

C. nemoralis: Larvae occurred on grass heath and cultivated ground.

C. problematicus: Larvae were found only in scrub and bracken areas.

Leistus ferrugineus: Only a few larvae were taken and showed the same distribution as those of C. problematicus.

Nebria brevicollis: The larval habitat is discussed in Section C. The majority of larvae were taken in beech litter.

Notiophilus biguttatus: Large numbers of the larvae were trapped in beech litter, occasional individuals could be found in scrub and bracken and one specimen was recorded from a cultivated field.

Loricera: Larvae appeared to be equally numerous on the grass heath and in woodland.

Harpalus rufipes: Larvae were common both on the heath and in cultivated land.

H. affinis: Larvae were only recorded from cultivated land, where they were frequent.

Amara species: Larvae were taken only on cultivated ground and grass heaths. They cannot be determined below the sub-genus, but the possible larval habitat of A. lunicollis and A. communis is discussed in Section C.

P. melanarius: Larvae occurred equally in grass heath and cultivated ground.

P. Madidus:) The distribution of larvae of these two species is dealt
) with in Section C; in both cases it follows adult
Abax:) distribution rather closely.

In these 14 species the distribution of the larvae appears to be very similar to that of the adult beetles. However, although there is no evidence here of seasonal migration or even large scale dispersal, the possibility must be considered. Van der Drift (1951) found larvae of Carabus problematicus occurred on the edges of woodland while the adults were generally distributed within it, implying some dispersal from the larval habitat. Dawson (1957) working with small adult overwintering species of Agonum and Pterostichus, found that the adults hibernated in grass-tussocks, accumulations of litter and piles of cut-reeds, moving out into open parts of the fen in the spring, while the new generation of adults returned to shelter in the autumn. Kabacik (1957) recorded Carabus arcensis in Poland migrating from damp shaded forest areas to dry and sunny ones during the second part of the annual period of adult activity.

d) Temperatures in vegetation types.

The preferred temperatures and humidities of Carabid species and the ranges which they are capable of withstanding have not been studied in

the present work. Problems of conditioning mentioned in A III 2) suggest that this would require elaborate investigation. However, the work of Tipton (1960) and others cited in A II 1) shows that there is some relation between the preferenda and performance of species and the physical properties of the typical habitat.

Hughes (1955) and Fewkes (1958) discuss the measurement of micro-climatic factors within the Silwood grass heath. This is complicated by vertical gradients of temperature and humidity which may become inverted after dusk or sunrise. In Section A III 2) it was suggested that different Carabid species may move at different levels in the grass heath, and Kabacik (1957) found that the same applies to certain woodland species in leaf litter. There is therefore little advantage to be obtained from attempts to record temperature and humidity extremely accurately, and the measurements below merely demonstrate the differences between the habitats studied.

To measure daily fluctuations in temperature two mercury/steel thermographs were available. After their reliability had been checked at the same temperature, they were used to compare ground temperatures on the litter covered floor of beechwood, in grass heath and on cultivated ground with a slight cover of weeds, each possible pair being compared in turn. Temperatures were measured $\frac{1}{2}$ inch below the soil or litter surface, as appropriate, to avoid direct insolation. In each case recording was continued for three days. Figure 18 shows the mean of the three recorded temperatures at two-hour intervals for the three pairs of comparisons.

This shows that the amplitude of the daily fluctuation is considerably greater in grass heath and arable land than in woodland, and this can be

attributed to the damping effect of the woodland canopy (MacFadyan 1957). In the two grassland habitats the maximum temperature usually occurred at about 2 p.m. (B.S.T.) while the minimum fell between 4 and 6 a.m. Woodland showed a time lag of several hours, the maximum temperatures being recorded from 4 to 8 p.m. and the minimum between 4 and 8 a.m.

Differences between grass heath and arable land are less obvious; the timing of the maxima and minima are the same, but slightly higher temperatures seem to be reached on the arable land. However, the measurement of temperature at a soil-air surface is extremely critical being complicated by steep gradients and, as far as temperatures near the surface of the soil are concerned, the recording instruments used are capable of little more than showing general woodland-grassland differences. For the same reasons humidity differences between the habitats have not been demonstrated here.

e) Habitat and the food of Carabidae.

Knowledge of feeding habits is of significance in discussing distribution in relation to vegetation, and the food of Carabidae can be reviewed briefly here. What is known of the feeding habits of the British species has been summarised by Davies (1953 and 1959(a)), and Skuhravy (1959) has attempted the quantitative assessment of seasonal and specific differences in the food of arable land Carabidae in terms of gut-content frequency.

Whenever possible feeding has been observed both in the field and the laboratory at Silwood and this has confirmed the work of the authors cited above. Many species are omnivorous, although there are exceptions

with specialised requirements, such as Cychrus rostroides which feeds on molluscs (West 1942) and Harpalus rufipes, a plant feeder with a preference for the seeds of Chenopodium album L. (Briggs 1957).

In general, however, it may be said of the major taxonomic groups that the Carabini are mainly predacious, the Pterostichini omnivorous, some species tending to be predators, for example Abax, while others may be almost exclusively phytophagous such as Amara species, a habit shared with many of the Harpalini. There is a tendency for the woodland and generally distributed species to be predators, while the grassland species are frequently plant feeders; this is particularly noticeable with the exclusively grassland genera Amara and Harpalus, which is only to be expected as living plant material is rare in a litter covered woodland floor. However, in some cases this plant feeding habit should not be over-emphasised. The idea has persisted that the Carabidae were almost exclusively predators, Fowler (1887) stating that "In habits they are predaceous and carnivorous". This has been dispelled by the work of Lindroth (1945) and Davies (1959) but there is now a tendency to regard many species, of the genera Amara and Harpalus for example, as feeding solely on plant material. But Davies records predation in Amara communis and Gabbutt (1959) suggests that Ophonus (Harpalus s.l.) species, Amara plebeja and A. tibialis prey on early instars of Nemobius sylvestris (Sosc.), while Skuhravy regards the majority of common species of cultivated land as predators. At Silwood Amara lunicollis was observed feeding on the Collembolan Podura longicornis Muel.

It seems, therefore, that the majority of Carabidae are omnivorous, although there remains a close relationship between habitat and the type of food most frequently eaten, apparently depending on availability rather than preference.

3) DISCUSSION.

It has been shown that the Silwood Carabidae considered in the present study are divisible into three groups: generally distributed, woodland, and grassland species. The woodland group is further divided into those species found only in litter, for example Notiophilus rufipes and Calathus piceus, and a less easily defined group which in one set of observations was found in bracken. However, they also occur in other types of vegetation associated with woodland, and it was suggested that their distribution might be centred on the edge of woods. But this group is not typical of the Holcus - Dactylis grassland on the extreme borders of woodland, and perhaps these Carabidae may be regarded as properly belonging to scrub, which is usually found on the edge of woodland. However, the Carabid fauna of scrub has not been extensively investigated, and such trapping as has been carried out there (for example the sycamore litter trap - table 22), has shown a mixture of true woodland, 'bracken' and grassland species, which is attributed to the presence of pure litter conditions, scrub and open grassy spaces in a small area.

Similarly the grassland species occur in different proportions on grass heath and arable land. However, the fact that many of the species can see and avoid traps, and differences in the ease of movement of Carabidae over bare soil and grass heath precludes detailed comparison of grassland pitfall catches.

However these minor distinctions of habitat remain subordinate to the initial three-fold division. In the case of ground-living arthropods such as Carabidae it is very frequently difficult to decide whether

distribution is determined by the vegetation and its associated ground fauna, flora and microhabit, or by the edaphic and climatic factors which determine the vegetation. In this instance no such problem arises if the heath and woodland Carabidae are considered, as it has been shown in Section B II 1) that the presence of either heath or woodland is determined by two factors which cannot be held to influence Carabid distribution. These factors are grazing (or the felling of trees and cutting back of scrub by man), and time, one plant community gradually being invaded and superseded by another. Neither of these can influence Carabid distribution directly, which must therefore be determined either by properties of the vegetation itself, the physical environment produced by any given type, or associated food organisms or predators or parasites. Although no laboratory experiments have been carried out here on the temperature and humidity requirements of Carabid species, available information on the subject suggests that the most important property of a type of vegetation is the microclimate near the ground surface.

Tischler (1955(a)), after considering arable fields where Carabidae form an important part of the surface fauna, concluded that "Animals living on the surface of the ground at least are more influenced by the edaphic conditions than by the covering of vegetation".

On the single soil type of the drier parts of the Field Station, however, this generalisation does not apply. Such differences in edaphic conditions as occur are restricted to the surface, and are directly related to the vegetation type. The Carabid habitats considered at Silwood show a series of increasing litter cover, from cultivated land where there is none,

through grass heath to woodland where fresh and decomposed litter may be several inches deep above the mineral soil.

Williams (1959) found that the distribution of captures of Carabid species in pitfalls in woodland and grassland could be related to a series representing the degree of development of the litter layer. The general distribution of species agreed with their habitats as described at Silwood, but in the absence of detailed work on temperatures and humidities in litter, it is not possible to ascribe such distributions to any specific properties of the habitat.

III. DAILY CYCLES OF ACTIVITY.

1. Introduction.

A number of those workers studying the ecology of Carabidae have dealt, if only briefly, with the time of activity of various species. Tischler (1955(a)) found that species which are shining and brightly coloured are typically diurnal, while duller and black species are nocturnal, and described differences in the habitats of the two groups. Park (1940) and Williams (1959(a)) have considered the significance of rhythms of activity as aspects of community organisation.

Tipton (1960) described daily cycles of activity in the nocturnal species Nebria brevicollis, where there is an inherent rhythm which is gradually lost in constant darkness or light, and in the diurnal Pterostichus caerulescens; In the latter the rhythm is apparently exogenous and determined by light intensity. Kirchner (1960) investigated Carabus nemorali C. violaceus, C. problematicus, Harpalus rufipes, Pterostichus niger, P. melanarius, P. madidus and Abax parallelopipedus in Germany, concluding that light was the most decisive factor in determining times of activity. Williams (1959(b)) related daily cycles of activity in P. madidus to the interaction of intrinsic rhythms and external influences. Harker (1958) suggested that the majority of animals possess a 24-hour cycle of activity, although in some social and subterranean insects it is not apparent, and infers that it is endogenous.

Cloudsley-Thompson (1961) has reviewed recent work on daily rhythms of activity in insects, concluding that even among closely related forms factors determining activity times are extremely diverse. Apart from the

interest of analysing these effects, studies on the time of activity of Carabid species are relevant to this work in that the climatic factors liable to limit the level of activity in any situation will vary with the daily time of activity.

Here the times of Carabid activity were investigated by direct observation, although other workers have used a variety of devices to record movement in arthropods of the same order of size. One of the simplest methods involves an aktograph based on that described by Edney (1937) where the experimental animal is confined within a pivoted chamber which tilts with movement across the point of balance. Harker (1955) attached a thread to the pronotum of Periplaneta americana through which activity was recorded. Williams (1959(b)) and Tipton (1960) restricted Carabidae to a circular runway ac ross which a beam of red and infra-red light was focussed on a photo-transistor. Current changes in this caused by the passage of the beetle were amplified and recorded.

These methods have the disadvantage that only one individual can be investigated at a time and none is applicable to the smaller Carabidae, such as Bembidion species. Those methods which use a small chamber or arena have the further disadvantage that they offer an extremely unnatural environment. Attempts were made to use a tilting aktograph in the present work but it was found that the majority of Carabid individuals tested would remain motionless in one corner of the activity chamber throughout 24-hour periods.

Kirchner (1960) investigated Carabid activity rhythms by the method of simple observation as used here and by confining a number of individuals

to a container with wooden floor, their movements being recorded through a microphone. However, the disadvantage here is that no distinction can be made between occasional movements by a beetle at rest and locomotor activity. In the other methods above only active movement which carried the individual around, or from end to end of the activity area are recorded.

2) Methods.

In the present work Carabidae were kept in glass jars 8 inches high with a diameter of 6 inches at densities of 2-15 per jar depending on the size of the Carabid; small species such as Notiophilus and Bembidion species were kept in 2 lb jam-jars. Jars were filled to a depth of 2-3 inches with leaf litter, grass or sandy soil and closed with glass lids to conserve moisture. Water was added occasionally to maintain the humidity at approximately the levl of species' natural habitats.

Food in the form of chopped earthworm, blow-fly and tenebrionid larvae, raw fish, slugs, small caterpillars, Collembola, grass seed, fungi an pieces of apple, was added as appropriate for the species. More than sufficient was always present to avoid hunger effects and no observations were made within one hour of the addition of food. It was found that under these conditions cultures of all the species used could be maintained for at least four weeks with negligible mortality.

The jars were kept in the open air, initially in a shaded yard, and later in shade in an insectary. They were subject to changes in temperature and illumination which approximated to those in the field. The temperatures within the jars showed a time-lag of $1^{o}F$ behind changes in ambient temperatur

The daily fluctuations in temperature within the jars in both cases, were most similar to those found in woodland (see B II) although in the culture-jars mean temperatures were somewhat higher. For example the mean minima and maxima in jars in the insectary in August 1960 may be compared with temperatures in the field (table 21).

TABLE 25. Mean temperatures (^{o}C) 16-18/8/60 at a depth of $\frac{1}{2}$-1 inch below the ground surface in woodland, grass heath and insectary cultures.

Mean Temperature		Grass heath	Woodland	Insectary
Maximum	Temp.	19.0	13.5	14.0
	Time (B.S.T.)	2 p.m.	4-6 p.m.	5-7 p.m.
Minimum	Temp.	10.5	8.5	11.0
	Time (B.S.T.)	6 a.m.	6-8 a.m.	6-8 a.m.

No differences could be found in air temperatures in the yard first used and in the insectary.

These effects can be attributed to the secluded position of the cultures, out of direct sunlight, delaying and damping down the daily rise and fall in temperature.

The main purposes of these observations was to discover what proportion of species' activity occurred in the day and night; no attempt has been made to separate from any inherent rhythm the effects of extraneous influences normally experienced in the field, hence the position of the jars in the open air rather than in a controlled laboratory climate.

The number of Carabidae seen on the surface in a jar at any time was taken as a measure of the activity of that sample. This agrees with the habits of all Carabidae so far identified as they retire under litter or into burrows during their inactive period, and emerge on to the surface when active. It should be stressed that this method does not give a direct measure of either locomotor activity or the energy expended in it.

The sex ratio in the jars for any species was arranged to correspond with that found in the field.

The jars were visited and activity recorded at irregular intervals throughout the day and night over periods of one to three weeks. Observations were made in red light after dark. From this values were obtained for the number of each species active per visit per hour, and this is expressed as a percentage of the maximum possible activity in the accompanying figures and tables. The results shown below were checked by visiting pitfalls throughout the day and night and noting at which periods species were active. The usefulness of this check is limited by the fact that diurnal species which in the day may see and avoid pitfalls will, if active at night, be trapped in numbers larger than their level of activity would warrant.

3) Results.

a) Times of activity of species.

The following species were investigated:

TABLE 26.

	16 - 25/10/58	23/4 - 7/5/59	25 - 31/7/59	8/6 - 1/7/60	11 - 19/8/60
C. problematicus	(X)	X			
C. violaceus					X
C. nemoralis				X	
Cychrus		X			
N. brevicollis	(X)	X			
Notiophilus substriatus		X			
N. rufipes				X	
N. biguttatus		X			
L. pilicornis		X			
A. flavipes		X			
B. lampros		X			
Badister lipustulatus				X	
H. affinis				X	
H. rufipes			X		
A. communis				X	
A. lunicollis			X	X	
S. pumicatus				X	
P. caerulescens		X			
P. niger	X	X	X		
P. melanarius	(X)		X		
P. madidus	X	X	X		X
A. parallelopipedus	(X)	X	X		
C. fuscipes				X	X
C. melanocephalus					X
C. piceus			X		
Laemostenus terricola					X
Agonum assimile		X			
A. ruficorne		X			
A. dorsale		X			

During the first series of observations in October 1958 the numbers of some species kept in jars varied, and it is only possible to show the duration of the active period, and they are bracketed in table 26. In later experiments some species were only brought up to maximum numbers during the course of observations; this is shown in the appendix tables and corrections are made in the calculation of percent activity.

Results are given in appendix tables 18-30 and figures 17-31.

On the basis of this evidence it is possible to distinguish three types of activity pattern, nocturnal, diurnal, and both day and night activity. The Amara species and Pterostichus madidus fall in the last category and were inactive only between 4 and 9 a.m.

b) Factors affecting times of activity.

Density. For every species the densities in jars were higher than those observed in the field during their annual periods of adult activity, and possible effects of this on the distribution of activity were investigated.

In July 1959 the activity of P. madidus was observed at densities of 5, 10 and 25 per jar with a replicate at each density, (figure 24), and for each density a value for the total percentage activity can be obtained (table 27).

TABLE 27. Activity of P. madidus at densities of 5, 10 and 25 individuals per jar. July 1959. 70 visits.

Density (No./jar)	5	10	25
Total No. observed active	68	47	123
No. of P. madidus	10	20	50
100% activity. (No. P. madidus x No. of visits)	700	1400	3500
% activity observed	9.7	3.3	3.5

Between 1/11/60 and 7/11/60 the activity of N. brevicollis was studied at densities of 4, 8 and 12 per jar, with replicates at the two lower densities. Results are shown in table 28.

TABLE 28. Activity of N. brevicollis at densities of 4, 8 and 12 individuals per jar. November 1960. 20 visits.

Density (No./jar)	4	8	12
Total No. observed active	98	138	95
No. of N. brevicollis	8	16	12
100% activity. No. N. brevicollis X No. visits	160	320	240
% activity observed	61.2	43.1	39.6

In each experiment activity was highest at the lowest density and crowding appears to inhibit movement. However figure 24 shows that in P. madidus the distribution of activity throughout the 24-hour cycle was similar at each density, and although the latter appears to be a factor determining the level of activity, it does not affect its general pattern.

Hunger. In the 1958 observations it was noticed that if food was withheld from cultures of Pterostichus niger or Abax during one nocturnal period of activity occasional individuals were active during the following day, when several would emerge onto the surface outside the normal active period if chopped earthworm was offered. The same was noticed by Williams (1959(b)) in P. madidus. For this reason a supply of food was always present in the jars.

Habitat. Williams (1959(b)) found that in grassland P. madidus tended to be diurnal and in woodland nocturnal, and the same applies to this species

at Silwood. Kirchner (1960) however, recorded it as being nocturnally active with a peak at dusk in crop-fields in August in western Germany.

Between 16/8/60 and 20/8/60 the times of activity of P. madidus from woodland and grassland were compared under insectary conditions; 15 individuals divided between three jars, from each habitat were considered. Comparisons may be made for the distribution of activity during the first 48 hours, (after an initial six hours for the beetles to find refuges and settle), during 48 hours after four days in the insectary and for the following 24 hours. Values were obtained for the level of activity between noon and 8 p.m., and 9 p.m. and 3 a.m. (B.S.T.). The period 3 a.m. to noon has not been considered as this is when temperature is liable to limit activity. Results during the hour between 8 and 9 p.m. have been rejected as it covered dusk when both nocturnal and diurnal Carabidae are active. Results are shown in table 29.

Between 6 and 54 hours after the beginning of the experiment there was negligible diurnal activity in the woodland specimens, while those from grassland showed a more equal distribution of activity, although again a higher level occurred at night. Williams (1959(b)) found rather less nocturnal activity in P. madidus in open country, and the relatively high levels here in grassland specimens may be an immediate response to the fact that insectary temperature changes approached those of woodland. After 4-6 days in the insectary the woodland beetles showed the same activity pattern as at the start of the experiment but those from grassland relatively less diurnal activity. On the last day the habitat difference had almost entirely disappeared. The P. madidus specimens whose daily activity is illustrated by figure 24 came from both woodland and grassland habitats and this will explain the duration of the active period.

TABLE 29. Activity of P. madidus from grassland and woodland. August 1960. Three jars of 5 individuals from each habitat. Results for each habitat combined.

1 = No. observed active.
2 = Maximum possible (No. P. madidus x No. observations).
3 = Observed % activity.

			B.S.T. noon - 8 p.m.	9 p.m. - 3 p.m.
6 - 54 hours	Grassland	1	32	73
		2	155	150
		3	20.6%	48.7%
	Woodland	1	1	94
		2	135	135
		3	0.7%	69.6%
96 - 144 hours	Grassland	1	16	33
		2	175	100
		3	9.1%	33%
	Woodland	1	3	53
		2	175	100
		3	1.7%	53%
144 - 168 hours	Grassland	1	1	34
		2	80	80
		3	1.2%	42.5%
	Woodland	1	0	39
		2	80	80
		3	0%	48.7%

Temperature. Tischler (1955(a)) noted that in the field high temperatures may stimulate nocturnal Carabidae to be active in the day, and diurnal ones to continue their activity into the night. Occasionally on warm afternoons at Silwood nocturnal Carabus, Pterostichus and Harpalus species were seen crossing paths and bare ground, and in the July 1959 activity

experiments single individuals of Harpalus rufipes and Abax were active from time to time between 9 a.m. and sunset.

As high temperatures stimulate activity low temperatures inhibit it; thus in July 1959 a high level of activity persisted throughout the night in P. madidus, P. niger and Abax (figures 24, 25, 27), while in spring 1959 when the monthly mean temperature was some 8°F lower (44°F as opposed to 52°F) activity before dawn was very much reduced.

Fluctuation in humidity has not been considered in the present work as a factor determining periodicity of activity, nor has it been included in the studies by other workers cited in this section. However, relative humidity usually varies inversely with temperature, and these effects must be closely linked.

Light. In the field light is not a factor which is liable to cause any variation from day to day in either the level of activity or its distribution between day and night; it is, however, the most important factor in determining the basic rhythms of activity. This has been shown by Kirchner (1960) for eight species of nocturnal Carabidae, and this is in accord with the easily demonstrated negative phototaxis shown by such species. Tipton (1960) has shown that light is also the most important agent in the establishment of a daily rhythm in Pterostichus caerulescens, a diurnal species which apparently possess no inherent rhythm.

However, it will be suggested below that daily cycles of activity determined by natural changes in light intensity may be considerably modified by fluctuations in temperature.

Discussion.

Factors which affect daily cycles of activity produce changes in the level of activity and by impinging on one part of the cycle more than on others may also lead to variation in the pattern of its distribution between day and night. The majority of Carabidae investigated here can be classed as diurnal or nocturnal although in the case of a few species the daily period of activity covers parts of both the day and night. For them the various factors considered in the previous section, (III 3) b)) may be examined as agents determining the periodicity.

Differences between woodland and grassland in the means about which temperatures fluctuate, and the amplitude of fluctuation are described in Section B II (2). In grassland the high maximum temperature which is reached in the early afternoon obviously favours diurnal activity, while in woodland the ground maximum may not occur until almost dusk after which the rate of fall of temperature is slow as compared with grassland, and in such conditions a higher degree of nocturnalism is to be expected. In the insectary the amount of fluctuation was similar to that found in woodland, and the maximum occurred at approximately the same time, although temperatures tended to be rather higher; this also favours nocturnal activity.

In the field the two Amara species are essentially diurnal; none was taken at night during day and night visits to traps; Williams (1959(b)) only trapped A. communis during the day, and in the field both species have frequently been observed moving in daylight. However, in the 1959 July, and 1960 June activity observations they showed as much or more nocturnal as diurnal activity. This can be attributed only

to temperature conditions in the insectary for these species inhabit only grassland and there is thus no question of experimental material coming from mixed sources as in P. madidus.

Grassland specimens of P. madidus in the August 1960 habitat experimen (table 29), under insectary conditions, assumed the same periodicity as those of woodland in seven days; this again would appear to be a temperature effect The corollary to this proposition is that diurnal activity in this species in grassland is also determined by the habitat's temperature properties. However, the period of a week required by grassland specimens to become active only at night suggests the presence of an inherent rhythm, and Williams (1959(b)) has suggested a mechanism by which this is reset according to habitat.

In woodland the species is nocturnal, time of activity being determined by a 24-hour inherent rhythm and inhibition of movement by light; minor peaks of activity occurred every four hours. In grassland a relatively high proportion of the total activity of surface-living invertebrates is diurnal (Williams 1959(a)), and he he suggests the nocturnal habit in the predacious P. madidus will lead to hunger; this appears to overcome inhibition by light and permits diurnal feeding activity, the resulting cycle of nocturnal hunger and diurnal satiation allowing the establishment of a new rhythm. However, it is possible that temperature is also a factor determining the time of activity of this species. Work on habitat (BII, CIII) suggests that P. madidus is essentially a grassland species. In Section BIV it is argued that the total diurnal activity of the grassland invertebrate fauna equals the nocturnal and one must question Williams' premise that nocturnal activity by P. madidus in grassland would lead to hunger.

In contrast Tipton (1960) working with the allied species P. caerulescens, which is diurnal, found no evidence of an endogenous rhythm of activity, periodicity being determined by light; however, temperature effects were not studied.

Kirchner (1960) investigated temperature, light and combinations of the two factors in determining rhythms in a number of nocturnal Carabidae, and concluded that light was of the greatest importance in determining times of activity. But in a 24-hour experimental day his temperature fluctuations consisted of rapid changes from 15°C to 25°C, the low temperature coinciding with the dark period. This is very different from the woodland conditions described here where there is a lag of several hours between maximum light intensity and maximum ground temperature. However, some species, (H. rufipes. P. melanarius and A. parallelopipedus) showed a greater response to temperature than others (C. violaceus and P. niger).

There appears to be a continuous range between such nocturnal species as N. brevicollis and C. violaceus, with a well-defined inherent rhythm of nocturnal activity and P. caerulescens and the Amara species which rapidly alter their activity pattern with changes in light intensity and temperature respectively. Among the species investigated several here may be included in the same group as P. madidus and Amara species and described as plastic in their periodicity of activity. They are species which may be expected to show variation in their rhythms in the field in response to changes in the environment. Species whose patterns are modified experimentally by manipulation of light intensity are not liable to be subjected to such changes in the field and are not included in this group. Certain species in which there is some doubt as to the typical time of activity are

included however.

Loricera pilicornis was found to be diurnal in the 1959 spring observations and this agrees with its habit in the field at Silwood. Kirchner (1960), however, found that the species was nocturnal in western Germany. Harpalus affinis and Agonum dorsale were nocturnal under insectary conditions and Kirchner trapped them mainly at night, but both sspecies have frequently been seen active on cultivated ground in the day. A further species which may be added to this group is Agonum mülleri. Although not among those species for which 24-hour percentage activity figures are available, observations in the field and the laboratory suggested that it was diurnal; however, between 14/7/60 and 17/7/60 five individuals were trapped at night between sunset and sunrise, and four in the day, while Kirchner trapped one in the day and seven at night.

Carabus nemoralis shows a different type of plasticity; Krumbiegal (1932) describes the species as nocturnal in the north and east of Europe and diurnal in the south. Hikimiuk (1948) found it to be nocturnal near Moscow, as did Kirchner near Cologne. At Silwood also it appears to be strictly nocturnal.

The Carabidae investigated at Silwood may be divided among the three groups as in table 30 according to their diel activity. In the field those species defined as plastic will tend to be diurnal in grassland habitats.

TABLE 30. Classification of Silwood Carabid species according to activity times.

Nocturnal	Plastic	Diurnal
C. violaceus	L. pilicornis	N. rufipes
C. problematicus	H. affinis	N. substriatus
Cychrus rostoides	A. lunicollis	N. biguttatus
N. brevicollis	A. communis	A. flavipes
Badister bipunctulatus	P. madidus	B. lampros
H. rufipes	Agonum mülleri	P. caerulescens
P. niger	A. dorsale	
P. melanarius		
A. parallelopipedus		
S. pumicatus		
Laemostenus complanatus		
C. fuscipes		
C. melanocephalus		
C. piceus		
Agonum assimile		
C. nemoralis		

B IV. THE RELATION BETWEEN ACTIVITY AND HABITAT IN CARABIDAE.

The daily and annual cycles of adult activity of 26 species of Carabidae have been described and are related to habitat in table 31 where overwintering stages are also shown.

From this it is evident that there is a close relationship between adult over-wintering, adult activity early in the year, and diurnalism. Of the 11 adult-overwintering species considered here only two are nocturnally active, while of 15 larval-overwintering species 13 are nocturnal. This is further illustrated by figure 32 and appendix table 31 which show that the highest percentage of the total catch of diurnal species occurs from April until June, while the maximum catches of the woodland species occur later and are distributed between May and the end of October.

There is a similar, but less well defined relationship between life history and habitat: of the woodland species only one third (3/9) overwinter as adults, and the numbers of spring, summer and autumn species are respectively 2:4:3. In contrast more than a half of the grassland species overwinter as adults ($^{6}/_{11}$), and the spring, summer, autumn proportions are 5:4:2.

The relation between habitat and daily time of activity is best indicated by table 32, where the number of species of each activity type in each major habitat group are shown (a). The widespread species occur in both habitats and may be added to both woodland and grassland groups, and from conclusions reached in Section B III, the plastic species may be considered to be predominantly nocturnal in woodland and diurnal in grassland ((b) grouped data).

TABLE 31. Habitat, activity and life history of Carabid species.

Species	Habitat	Daily Activity	Annual Activity	Life History
N. rufipes		D	S	a
C. piceus		N	M	l
N. brevicollis	L	N	A	l
Cychrus		N	M	l
N. biguttatus		D	S	a
Abax		N	M	l
C. problematicus	B	N	A	l
L. ferrugineus		N	A	l
Stomis		N	M	a
P. niger		N	M	l
C. violaceus		N	M	l
Synuchus		N	M	l
Loricera	W	P	S	a
N. substriatus		D	S	a
P. madidus		P	M	l
C. nemoralis		N	S	a
A. communis		P	S	a
A. lunicollis	M	P	M	a
C. fuscipes		N	A	l
C. melanocephalus		N	A	l
H. rufipes		N	M	l
H. affinis		P	M	l
P. caerulescens		D	S	a
B. lampros	A	D	S	a
P. melanarius		N	M	l
A. dorsale		P	S	a

Woodland (L = Litter, B = Bracken, W = Widespread)
Grassland (H = Heath, A = Arable)

N = Nocturnal, P = Plastic, D = Diurnal

S = Spring, M = Summer, A = Autumn

a = adult, l = larval over-wintering

TABLE 32. Daily distributions of activity in Carabidae from woodland and grassland habitats. (See text for explanation).

(a) Observed data

Habitat group	Activity type Nocturnal	Plastic	Diurnal
Woodland spp.	7	0	2
Grassland spp.	5	4	2
Widespread spp.	3	2	1

(b) Grouped data.

Habitat group	Activity type Nocturnal	Diurnal
Woodland spp.	12	3
Grassland spp.	8	9

On this basis table 32 shows that woodland supports a majority of nocturnal species, and in grassland the common species investigated are roughly equally divided between nocturnal and diurnal activity.

Tischler (1955(a)) found similar differences when comparing the Carabid fauna of sandy and loam fields; diurnal species were less abundant on the latter, and this can be attributed to the thermal properties of the two types of soil. Heydeman (1953) (cited by Tischler) found that the differences between the two soil types were similar to those described here between woodland and grassland, daily maximum temperatures being higher on the lighter soil, and occurring sooner than on loam. On warm nights nocturnal activity was twice the diurnal level on both soils, but while on a cold night on a loam field activity equalled the daily level, on a sandy field it only attained half that intensity. He recognised that on cold nights the activity of the surface fauna is more strongly depressed on a sandy field than on a loam one. The present observations on daily times of activity imply that with the same sort of temperature differences the daily fluctuations in grassland have a greater effect on activity than those in woodland.

Diurnalism is discussed from a different point of view by Williams (1959) who used pitfall traps to compare the amount of diurnal and nocturnal activity of invertebrates on the floor of woodland and in open scrub, finding a more completely symmetrical distribution of activity over the 24-hour cycle in woodland. This was considered confirmation of Park's (1940 hypothesis that in an advanced animal community activity is symmetrically disposed throughout day and night allowing efficient exploitation of resources, while in the more primitive state activity is asymmetric.

Here the more advanced animal community was held to be associated with the more mature woodland community with a well defined litter layer and layering of the vegetation, while the supposedly less advanced animal community occurred in the less mature open scrub.

It has already been suggested in this work that pitfall traps do not give a reliable measure of total locomotor activity in a habitat when a number of invertebrate groups or species are involved, but apart from this Williams' conclusions conflict sharply with observations made in the present study. In both cases it was found that far more diurnal activity occurred in open or grassland habitats than in woodland, but Williams found that the predominance of diurnal activity caused asymmetry in the open habitat. At Silwood it was only in the latter that there was any balance between nocturnal and diurnal Carabid activity. This can be illustrated by tables 33 and 34 where the catches of the 26 species are divided according to habitat and activity times. The observed catches are shown and for comparison are adjusted so that the total catch of nocturnal species equals 100.

In woodland and grass heath only occasional Carabidae were trapped which were not among the 26 dealt with here, and their incidence is negligible. On arable land the discrepancy between pitfall catches and soil samples has been discussed in Section A III 2, and here a number of diurnal species occurred which have not been included in this study. In table 34, therefore, the catch of diurnal species may be an underestimate of the total amount of diurnal activity.

However, the tables show that the Carabid fauna of woodland is predominantly nocturnal, while in grass heath and on arable land the catch is more equally distributed among nocturnal and diurnal individuals, especially if the plastic species are diurnally active in grassland.

Although only Carabidae are considered here they constitute a very large proportion of the invertebrates taken in pitfall traps, and all other elements of the surface invertebrate fauna would be required to show activity rhythms opposed to those of the Carabidae in order to disturb the general pattern shown in tables 33 and 34. Tischler (1955(a)) found that Carabidae formed 70% of the surface fauna in biomass on loam fields in Schleswig-Holstein, and at Silwood the only other groups which are more than very occasional in traps are, among the Coleoptera, Staphylinid adults and larvae and Cantharid larvae, with Lycosid spiders, Phalangids, Chilopoda, Diplopoda, Collembola and earthworms. In so far as the catch of pitfall traps can at all indicate the activity of a community, Carabidae alone may be taken as providing some index of its distribution.

The arable land traps were situated in Hill Bottom between crops and experimental plots on initially bare soil, later colonised by a pioneer plant community of rosette and semi-rosette hemicryptophytes and herbaceous chamaephytes.

The case here, therefore, is of a mature woodland plant community with a well defined litter layer supporting an animal population in which at least the Carabidae are largely nocturnal. In contrast in the pioneer plant community of sparsely weed-covered arable land, which was immature to the extent that even until the end of both summers bare patches of ground persisted, Carabid activity was equally divided between night and day.

TABLE 33. Catch of 23 traps 1958-60.

Habitat		Activity Nocturnal	Plastic	Diurnal
Woodland (Including bracken)	Observed catch	3480	781	42
	Corrected catch	100	22	1
Grass heath	Observed catch	415	1104	84
	Corrected catch	100	266	20

TABLE 34. Catch of arable land traps. 1959 and 1960.

Arable land		Activity Nocturnal	Plastic	Diurnal
Summer 1959	Observed catch	186	103	81
	Corrected catch	100	55	43
Summer 1960	Observed catch	113	108	109
	Corrected catch	100	66	67
1959 & 1960 combined	Observed catch	349	110	190
	Corrected catch	100	60	54

If Carabidae do not give a totally erroneous impression of community activity, this can only be reconciled with Park's (1940) hypothesis if it is considered that an advanced animal community can be associated with a primitive plant community.

Tipton (1960) compared aspects of the bionomics of Nebria brevicollis and Pterostichus caerulescens. He related his findings to Kennedy's (1928) suggestion that primitive insects possess a lower rate of metabolism than the more advanced and inhabit cool, damp situations with a low 'energy intensity'; the more advanced insect is to be found in high 'energy intensity' habitats with more insolation and higher temperatures.

Tipton showed that N. brevicollis, systematically the more primitive, occurs in woodland and is nocturnal with adult activity in the spring and autumn. The more advanced P. caerulescens is a diurnal inhabitant of more open areas and is active mainly in the summer. It is also more advanced, or at least more successful in its retention of water, wider tolerance of temperature fluctuations and its ability to modify the daily time of activity with changes in the environment.

However, the concept of a relation existing between the energy intensity of a species' habitat, and its level of evolutionary development seems to be of limited value. Various trends have been mentioned whereby Carabidae may show changes in life-history, habitat or daily time of activity in different parts of their European distribution. Carabus nemoralis is a nocturnal, or possibly plastic, grassland species at Silwood, but near Moscow is a strictly nocturnal inhabitant of woodland (Hikimiuk 1948), and in southern Europe becomes diurnal (Krumbiegel 1932). Such changes can be

related to physical properties of the habitat and the induced range of tolerance of the species; it occurs in grassland in Britain, but may be excluded from the habitat by low humidities in continental Europe.

However, Tipton's observations suggest that open habitats require a higher degree of special adaptation in their Carabidae than is necessary to those that inhabit woodland, and reports of concentrations of Carabidae are significant in this respect.

Schuler (1956) described two situations in which he found Carabidae to be unusually abundant, both in species and individuals. One was in a recently felled forest in which there was little ground vegetation but abundant cover in the shape of bark and branches; the other was beside a newly made road on initially bare ground among scattered bricks and road-making materials which had been abandoned. In both cases he attributed the numbers of Carabidae to a combination of four factors, of which the first two were considered the most important. They were:

1. The presence of cover.
2. Bare ground exposed to the sun.
3. Moist soil.
4. The absence of natural predators.

Schuler described the ideal Carabid habitat as 'les abis ensoleilles', that is an area of high insolation provided with refuges.

Similar concentrations of Carabidae have been recorded during the course of this work. One occurred at Silwood in July 1959 in the area of the arable land traps in Hill Bottom on sandy soil with a slight weed cover. Here were scattered bricks and small piles of pulled weeds from nearby plots,

and among them large numbers of arable land Carabidae were found, including aggregations of Harpalus affinis (Appendix 2).

The other was recorded in April 1960 near Fleet in Dorset and is described in Appendix 3. In each case both shelter and bare ground were present, the latter occurring as worn tracks and paths beside walls in the Dorset record. Townsend (1945) records a similar concentration of Carabidae on a tip of carbon refuse from a gas-works. This was sparsely covered with weed species which, with a number of large stones, provided cover.

These notes suggest that a certain combination of physical factors forms an extremely favourable habitat for Carabidae. This presumes that numbers are not controlled by the food supply or the incidence of enemies. In fact the majority of Carabidae are potentially omnivorous and except in unusually unfavourable areas food will be present. Detailed information on the extent of predation and parasitism on the group is wanting, but it is shown in the next Section that Carabidae are mobile insects, and their enemies must therefore possess at least equal mobility. They are thus unlikely to be distributed in the same pattern as Carabidae except to attack a pre-existing concentration.

Therefore these concentrations of Carabidae can be considered as mainly the result of a combination of shelter and bare ground. On the latter high diurnal temperatures will be reached favouring a high level of activity, while the shelter affords refuges for beetles during their resting periods, and under it both temperature and humidity will remain relatively high during any extreme fall outside. This will be particularly important to surface-living larvae.

The implication of Tipton's conclusions is that open habitats tend to be occupied by Carabidae with morphological and physiological adaptations to what may be an unfavourable environment for less specialised species. Schuler's observations on the other hand suggest that the open habitat, provided cover is available, favours most Carabidae.

While those Carabidae in open habitats must tolerate a more fluctuating environment and often low humidities, those with woodland habitats have a more stable enviroment. Nevertheless, both groups would appear to benefit from high temperatures and the high level of activity they permit. The combination of open spaces and cover seem to allow the presence of members of both groups to some extent, but is particularly favourable to open habitat species.

The present work and examination of other studies in the same field emphasise that, at least within any one of the habitats investigated here, Carabidae form a distinct ecological group. As adults they are all active within a restricted horizontal stratum of the habitat, where they form a large or even dominant part of the arthropod fauna. In any area a large number of species may occur all of which tend to have similar feeding habits, and to a large extent are equally influenced by the same physical properties of the environment. Consequently a habitat which is favourable to one species will be just as suitable for many others. In such circumstances inter-specific competition would be expected to occur, especially when the extensive coexistence of allied species at Silwood is considered.

For example, among the common Carabidae there are three species of

Notiophilus of which two occur in litter, and with Leistus species (Greenslade 1961), and Nebria brevicollis form a group of active woodland predators composed of the two closely related tribes Nebriini and Notiophilini. However, direct competition is avoided by size and life history differences, and by diurnal activity in Notiophilus and nocturnal in Nebria and Leistus. The larger Pterostichini form a similar group consisting of P. caerulescens and the less common P. cupreus, and P. niger, P. madidus, P. melanarius and Abax. Here the first and almost certainly the second, are diurnal grassland species with summer larvae, while the remainder overwinter as larvae, and except for P. madidus are strictly diurnal; of them Abax is a woodland species, while P. melanarius is most common in grassland. However, P. caerulescens and P. cupreus appear to make very similar demands on their environment, as do P. madidus, P. niger and P. melanarius, although here there are slight differences in habitat.

Harpalus rufipes and H. affinis are very similar in life-history and habitat and might be expected to compete. However, the diel activity of the latter is plastic or diurnal in the field, and that of H. rufipes nocturnal, and Skuhravy (1959) found that H. affinis is a more exclusive plant feeder. Briggs (1957) on the other hand could find very little difference between the two species.

On the sandy soil of Hill Bottom 17 Amara species were recorded, that is all those found at Silwood except A. praetermissa, and almost half the British species. Of these A. communis, A. lunicollis and A. convexior are closely related with similar life histories, food and habitats. However, although the periods of maximum adult activity of A. communis and A. lunicollis the most abundant species, both occur early in the year, they do not coincide.

There is therefore evidence that in some cases where a number of allied species appear to coexist they do not compete but occupy the same niche either at different times of the day or of the year, or their distributions are centred on different habitats. It is almost certain that even when no differences between allied species have emerged in this work they would be revealed by further investigation.

It is probable that such differences would be of two sorts. One is the relation between the physical tolerances and preferenda of species and minor variation in the climate of habitat. The latter will consist of a mosaic of high and low temperatures and humidities, and it is suggested that even in such a generally suitable habitat as one providing open ground and cover, some situations will favour individuals of one species more than another, so that each will have its small area of dominance. This would be particularly important in the large and varied Carabid fauna on the borders of arable land.

On less theoreticall grounds it can be suggested that competition is avoided by specialisation in the larval habitat or food requirements. There is evidence that the larvae are more restricted and less catholic than the adults. Whereas the imagines of all the 26 species studied occur in traps, many of their larvae do not. Larvae of Carabus species, L. ferrugineus, Nebria, Notiophilus biguttatus, Loricera, P. madidus and Abax were common in pitfalls, and those of H. rufipes slightly less frequent. However, larvae of P. caerulescens, P. niger, H. affinis, Amara and Calathus species and others were not taken in traps or were rare in them. This implies that larvae of the first group are active on or near the ground surface while those of the second live within the soil. Those of Amara species for example were abundant in soil samples from Hill Bottom in the summer of 1960 but during the

same period were very uncommon in traps in the same area. Van der Drift's (1951) observation that Carabus problematicus larvae are apparently restricted to the edges of woodland has been mentioned.

Briggs (1957) found that the preferred food of adult and larval H. rufipes was seed of Chenopodium album but the larvae were far more dependent on it. It is suggested below in section C that the distribution of A. lunicollis and A. communis is centred on patches of Galium hercynicum the adults appear to be omnivorous or general plant feeders, so this may suggest that the larvae feed on the Galium or its fallen seed. Abax adults are mainly, but not exclusively predacious, but the strongly pointed, sickle-shaped mandibles of the larvae are obviously suited to a purely predatory existence. . . .

However, the purpose of this section is to establish the most important ecological characteristics of Carabidae, that is to discover what attributes the species investigated have in common, rather than to describe the minor differences which determine the niches they occupy. In fact it has been established that the various species of ground-living Carabidae have much in common.

It is possible to distinguish major groups according to habitat, overwintering stage or daily activity, and to some extent to relate these groups to each other and to the systematic position of their members. But the relationsips are not consistent and therefore it is not possible to make an ecological classification on the basis of, for example, habitat or level of evolutionary development, which will satisfactorily include other factors such as life history or daily time of activity.

For example, in agreement with Tipton's (1960) conclusions the relatively primitive and closely allied Nebriini and Notiophilini are mainly woodland species at Silwood, but it has been pointed out that both diurnal and nocturnal species are included and they combine to exploit the smaller arthropods of litter throughout the year. Tipton's thesis that the primitive Carabid is associated with the low energy intensity habitat becomes even less tenable in this context when the related Nebriine Eurynebria complanata L. is considered, as it inhabits the very unfavourable and high energy intensity environment of arid sand-dunes. Similarly the Pterostichini are systematically more advanced and although they show the expected variation and adaptability in their daily activity cycles they are generally distributed among all habitats.

Therefore to attach special importance to one of several inter-related attributes of a species is of no general significance. This has been done by Williams (1959(a)) and Tipton (1960) and it has involved relating selected properties of species to pre-existing theoretical concepts of evolutionary development and community organisation. This is dangerous as such properties may vary geographically.

C. STUDIES ON SELECTED POPULATIONS.

I. Methods.

1) Marking Carabidae.

As Carabidae retire into soil and litter when inactive, spots of paint on the integument tend to be rubbed off, and Gilbert (1956), Briggs (1957), Dawson (1957) and Skuhravy (1957) marked them by cutting off or piercing the apex of an elytron. However, by this method the range of possible marks is restricted and it was found that a petroleum based 'dope' (Britfix Colour Dope; Humber Oil Co. Ltd., Hull) stayed satisfactorily on the elytra of Nebria brevicollis, and individuals of this species and Pterostichus madidus so marked showed no more mortality in insectary cultures than unmarked. In the field it was found that marks appeared to remain unworn for up to four months on Nebria, and although some marks were still present after twice this period it is probable that others had been lost.

On P. madidus, however, the marks were less permanent; this is a larger and more active species with a smoother integument. An experiment was carried out between 11/8/60 and 25/8/60 in which 10 male P. madidus were marked, each with 12 marks on the surface of the thorax and elytra, and the rate of loss of marks was recorded in an insectary culture. Results are shown in table 35 and figure 33.

During work on populations of this species from June to August 1960, a large number of individuals were marked and released in the field and the rate of loss of marks in recaptured individuals of both sexes may be compared with that in the insectary culture (table 36 and figure 34).

It was noticed that marks on the disc of the thorax and elytra were lost first, followed by those on the leading edges of the thorax and elytral

shoulders, while none of those placed on the apical declivity of the elytra showed signs of wear, although in the field they are no doubt eventually lost. In the insectary these posterior marks formed 17% of the total and in the field, where the numbers of marks carried by any individual averaged only 4-5, they formed 45%. If in figures 33 and 34 the trend of the rate of loss of marks is extrapolated it is seen that all but the two posterior marks (shown by the broken lines at 17% and 45% respectively) are lost by the fourth week after release in both cases.

During the summer of 1960, 700 P. madidus were marked with individual numbers by a system of colour and position, the two positions on the apex of the elytra being retained for date marks. This species occurs in red and black-legged forms and the leg colour and sex of each individual marked was recorded. This, in conjunction with the date-marks permitted individual identification of virtually all recaptures even four or more weeks after release when the majority of other marks had been lost. Whenever possible marks were renewed.

One advantage of the paint used was that it dried in a matter of minutes and Carabidae which were removed to the laboratory for marking could be returned to the field and released almost immediately. In the laboratory marking appeared to have no effect on their behaviour.

TABLE 35. Rate of loss of marks in an insectary culture of 10 P. madidus (♂♂) between 8/8/60 and 25/8/60.

No. of beetles.	Days after marking	No. of marks remaining.	Maximum possible	% remaining
10	0	120	120	100.0
"	3	117	"	97.5
"	8	92	"	76.7
"	10	72	"	60.0
"	15	42	"	35.0
"	17	34	"	28.3

TABLE 36. Rate of loss of marks in the field in P. madidus (both sexes) between June and August 1960.

No. of beetles.	Days after marking	No. of marks remaining	Maximum possible.	% remaining
10	0 - 5	41	47	87.0
14	6 - 10	56	63	88.9
8	11 - 15	23	34	67.6
3	16 - 20	8	12	66.7

2) Recapture rates and the analysis of release/capture data.

Marking and recapture affords information on density, natality, mortality and migration in populations and there are available a number of methods of analysis of the experimental data obtained. Most of these, however, have been empirically designed tp deal with a specific problem. They are reviewed by MacLeod (1958) and Turner (1960).

Turner showed that the precision of estimates is governed by the recapture rate. From MacLeod's survey it appears that no satisfactorily accurate estimates can be obtained from data which include extensive nil-recaptures. Most of the work described in Section C has been carried out on Nebria brevicollis and Pterostichus madidus and in 1959 preliminary experiments were carried out to determine the distances moved by these and other species, and the rates of recapture which can be expected.

Two plots of 20 pitfall traps within areas of 64 sq. yds. were laid out in beech litter and grass heath in South Lodge Wood and on Elm Hill respectively. These areas were selected as they provided the most extensive and uniform stretches of litter and heath as could be found. In South Lodge Wood/45 other traps within 50 yds. of the plot of 20 traps, and on Elm Hill there were 50 traps within 90 yards. Marked individuals were released within the plots and subsequent recaptures there indicated the persistence of the marked population, while those in the neighbouring traps demonstrated the distances which individuals are capable of travelling.

Recaptures within the release area are shown in tables 37 to 39, and also the dates of experiments, species involved and numbers released (the last bracketed).

TABLE 37. Recaptures of marked Carabidae in South Lodge Wood plot 19/6/59 - 26/6/59.

No. of nights activity after release	Nebria brevicollis (50)	Pterostichus madidus (15)
1	5	-
2	2	-
3	-	2
4	2	-
5	-	-
6	-	2
7	No further recaptures	

TABLE 38. Recaptures of marked Carabidae in South Lodge Wood and Elm Hill plots. 22/7/59 - 1/8/59.

No. of nights activity after release	South Lodge Wood		Elm Hill	
	Abax (12)	P. madidus (20)	P. madidus (20)	H. rufipes (20)
1	3	2	1	1
2	-	1	-	-
3	-	1	-	-
4	-	-	-	-
5	1	1	-	-
6	-	1	-	-
7	-	1	1	-
8	-	1	1	-
9	No further recaptures			

TABLE 39. Recaptures of marked Carabidae in Elm Hill plot. 28/7/59 - 10/8/59.

No. of nights activity after release	Pterostichus madidus (80)
1	2
2	1
3	No further recaptures

In all cases recaptures were slight and dispersal from the point of release was rapid, no recaptures being recorded more than eight days after release. The occurrence of marked Carabidae at a distance from the release points was even lower. In the June South Lodge Wood experiments one P. madidus and one N. brevicollis were recaptured after 4 nights of activity in traps respectively 36 and 30 yards from the release area. On Elm Hill in June 1959 many marked Carabidae liberated in an enclosed plot escaped; of these one N. brevicollis was recaptured in a trap 85 yards away one week later, and another occurred after four weeks at the same distance. No other distant recaptures were made.

These experiments do not indicate any persistence of a marked population about the point of release when there are no obvious barriers to movement. N. brevicollis is capable of travelling 85 yards in a week and P. madidus 36 yards in four days; mobility of this order, approximately ten yds. per day, in rather small marked samples of Carabidae is quite adequate to produce the low rates of recapture observed. In three days a sample of either of these species could be distributed over an area of nearly 3,000 sq. yds.

Various Carabidae, surplus from other experiments and laboratory cultures were marked and released in 1959, and with those from the releases described here make a total of 500; of these 25 were taken again in traps. This recapture of 5% compares with 7% reported by Gilbert (1956) for Calathus species, and similar figures are given by Dempster et al. (1959) for P. madidus, Nebria and Abax at Silwood, for Abax by van der Drift (1951), and for Pterostichus cupreus by Skuhravy (1957).

This recapture rate, and the inevitable incidence of nil-recaptures, precludes the application of such methods of analysis as those of Leslie and Chitty (1952) and Fisher and Ford (1947). For the same reason, unless very large numbers are marked, any other method will result in imprecise estimates of populations and of the rates of appearance and disappearance of active individuals from the area studied. The only way in which more accurate estimates can be obtained is by the pooling of data from successive releases and recaptures, but this involves considerable loss of information.

Where necessary the latter course has been followed, and trends in population-density investigated by a number of releases and recaptures. Migration has been followed independently by separate releases and attempts to trace movement directly by trapping marked individuals over a wide areas. In this way one can to some extent establish both rates of mortality and emergence of adults, and migration.

In fact it was found, with Nebria at least, that the population investigated provided recapture rates in excess of 5% owing to restriction of activity to a limited area of beech litter. Tipton (1960) estimated numbers in such a population of Nebria by the method of Fisher and Ford (1947). However, this requires the fitting of a death-rate which is presumed constant, and involves laborious calculation. In this case it was thought preferable to estimate population density by a simple Lincoln Index, using Bailey's (1952) correction for small numbers. This is a simpler process and allows a number of estimates to be made of the population on any release date. The variance of the mean of these values for any release was found to be lower than that obtained from a single release and recapture obtained by following

Bailey (1952). Migration was investigated both by the internal evidence from changes in the proportion of the population which was marked, and by marking and trapping elsewhere.

The methods of analysis used are described in detail where appropriate later in this section.

C II. Nebria brevicollis

1) Site of population studied.

It has been shown in Section B that Nebria brevicollis is a woodland species, at Silwood characteristic of beech litter, and the site selected for work on a population of this species was an expanse of litter on Wood Bank. This was approximately 2000 sq. yds. in extent and sloped gently S.S.W. from Elm Hill to the Marsh. Half this area was bounded by bracken and the remainder by a Holcus-dominated grass community, and bramble and low mixed scrub (Figure 35). It was selected for the uniformity of the litter floor and its isolation from other such litter-covered areas. The litter occurred under a stand of beech which was continuous laterally with mixed oak and beech under which occurred bracken and scrub. At the bottom of the litter area lay the marsh, beyond a strip of bracken; above it there was a small area of litter under beech, separated from the main area considered here by 50 yds. of scrub and grass, the latter dominated by Festuca rubra.

Litter depths and the frequency of plant species within the area investigated were plotted initially in October 1959 and again in more detail in July 1960. There was no significant change in plant or litter distribution during this period and the 1960 results are given.

The vegetation and litter were plotted by 10 random casts of a 9 x 9 inch quadrat within 10 yds. of each of a regular grid of 49 traps covering the whole area. Litter was defined as loose material which could be brushed off the soil surface with the hand, and in each quadrat the depth was measured with a probe to 0.1 inches. Plant species occurring in each quadrat were recorded and for the area around each trap the frequency of

any species or type can be graded. Appendix table 31 shows mean litter depths, and frequency of bracken, ground layer and field layer species. The ground layer consisted mainly of Holcus mollis but Deschampsia flexuosa and Agrostis tenuis also occurred. The field layer species, apart from bracken, were bramble, Chamaenerion angustifolium (L.), and young saplings of beech, sycamore and holly.

Four types of ground cover can be distinguished:

1) Bracken. Arbitrarily defined as those areas in which the frequency of Pteridium exceeded 20%. In them the ground layer was typically undeveloped and litter deep.

2) Low scrub. Areas dominated by field layer species, again defined as showing a frequency above 20%. Vegetation of this type was characterised by a vigorous growth of Holcus and frequently much litter.

3) Grass. Predominantly Holcus, but towards the bottom of the slope Deschampsia was dominant in small areas. The frequency of ground layer species was defined as above 50%.

4. Litter. This occurred in parts shaded by beech with only a sparse growth of Holcus, whose frequency was not more than 50%.

The last two vegetation types showed less litter accumulation than the first. The distribution of the four types is shown in figure 35 and variations in litter depth in figure 36; both figures also show the distribution of tree species and the association between beech and bare litter is evident. The figures show the increase in litter depth with vegetation cover, and the relation between litter, ground and field layer vegetation is further illustrated by table 40. This indicates the relative

absence of a ground layer under bracken and its contrasting abundance amongst other field layer species. The litter depths, combined with field observation, suggest that dead leaves are dispersed from areas with little vegetation cover by wind, and accumulate in bracken and low scrub.

In the autumn of 1959 a grid of 36 pitfall traps 5 yds. apart was placed as shown in figure 37; a further 35 traps were placed beyond them in the remainder of the litter area and in the surrounding vegetation. The plot was so designed that the grid catches would indicate the pattern of distribution of N. brevicollis in uniform beech litter, while the other traps indicated the density over the rest of the area. The main grid was placed within a stand of eight mature beech trees.

In early spring 1960, before trapping was restarted the traps were reorganised to form a single grid of 49 traps each 10 yds. apart, to give regular cover over the whole area (figure 37). This was based on the original plot and fortuitously no problems arose from selected trap positions being occupied by trees.

In 1959 trapping was carried out between September 25th and mid-November, the end the autumn activity of N. brevicollis, and in 1960 from April 20th to November 20th. In general traps were visited twice a week.

A general view of the plot is shown in photograph 1 (Appendix 5).

TABLE 40. Vegetation and litter depth on beech litter plot.

Vegetation	No. traps	Mean litter depth (inches)	Mean ground layer frequency %.
Bracken frequency > 20%	13	2.6	23
Other field layer spp. frequency > 20%	11	3.5	59
Bracken and other field layer spp. 0 - 20%	25	1.6	30
Ground layer frequency > 50%	9	1.9	
Ground layer frequency 0 - 60%	.6	1.4	

2) Results.

a) Distribution.

Some idea of the distribution of the population in the beech litter plot can be obtained from pitfall catches. The results of the trapping carried out in the autumn of 1959 and from May to November in 1960 are shown in figures 38 and 39, and in appendix tables 32 and 33. All unmarked Nebria were included, and marked individuals recaptured more than one week after release. This allows for dispersal among the population from the point of release. In the following sections, where work on dispersal is described, more stringent precautions are taken to avoid complications due to increased activity after marking; for the present purposes,however, it is sufficient to allow one week for the activity of marked individuals to return to normal.

The 1959 trapping showed that the population was largely restricted to the area of litter; the mean catch of litter traps may be compared with that of traps in bracken and scrub by the t-test (table 41). This shows that significantly fewer N. brevicollis occurred beyond the litter and grass areas, and is illustrated more clearly by the 1960 results in figure 39 and appendix table 33.

Figure 38 suggests that in 1959 either trap density within the grid reduced catches, or that the greater part of the population existed lower on the slope. In 1960, however, with a uniform trap density the general distribution of catches was the same; this is shown by table 42, where the catches of traps within the 1959 grid of traps and beyond, are compared for 1959 and 1960. If trap density did reduce catches within the grid in 1959, it could be expected that in 1960 catches in that area would be higher

TABLE 41. Comparison of catches of N. brevicollis in 1959 in traps in bracken and scrub with other traps.

	Traps in bracken and scrub.		9 traps at random in grass and litter.
No. traps	9		9
Catch	10.6		174
Mean/trap	11.18		19.33
S^2		15.65	
t		2.34	
Df		16	
P		<0.05	

TABLE 42. Comparison of distribution of N. brevicollis catches, 1959 and 1960, with reference to trap density.

		No. traps	Total catch	Mean/trap
1959	Grid traps	34	564	16.6
	Other traps	28	866	30.9
1960	Traps lying within 1959 grid	8	90	11.2
	Traps lying beyond 1959 grid.	21	340	26.2

Ratio of mean catches: traps beyond 1959 grid/trap within 1959 grid.

1959

$30.9 / 16.6 = 1.9$

1960

$26.2 / 11.2 = 2.3$

relative to the catches elsewhere. Traps in bracken and scrub are excluded from the comparison.

It is seen in table 42 that the ratio of mean catches: traps beyond grid/traps within grid is higher in 1960 than in 1959. This means that in 1960, with uniform trap density catches within the grid area were, in relation to catches elsewhere, lower than in 1959. There is no evidence therefore that trap density affected catch in 1959.

The figures show considerable variation in catches within the grass litter area, often between adjacent traps and this is most marked in 1960. This may be due to real differences in the density of Nebria, or to differences in the efficiency of traps.

However, in the 1959 grid the distance between traps was half that in 1960, and in the first case the differences between adjacent traps are least. In 1959 the grid traps showed areas of high Nebria density, and traps with high catches are in general separated from those with low by traps with intermediate catches. In 1960, within the 1959 grid area the same nodes of high density persist, being recognisable in the centre of the grid area, and in its bottom right hand corner on the figure, although in few cases were the same trap positions occupied in both years. The variation in catches of adjacent traps in 1960 can be attributed therefore to the distance between traps being such that gradients of Nebria density are not revealed as they were in 1959 with more traps closer together. The effect of variation in the efficiency of individual traps has not been further considered.

This population of N. brevicollis is apparently distributed in the litter and grass areas, with the highest density occurring toward the lower

part of the slope. The drawbacks to using pitfall traps for determining distributions have been discussed in Section A III and this apparent distribution must be considered in the light of the conclusions reached there.

An obvious factor which would affect catches is litter depth and the amount of ground vegetation, by restricting horizontal movement. Here this factor is probably not important, or at least does not conceal the real distribution, as extensive hand collecting in bracken and scrub areas revealed very few Nebria brevicollis. Further evidence for this statement is afforded by the distribution of Abax (Appendix table 33 and figure 56). This species occurred in the greatest numbers where N. brevicollis was lowest and it was almost entirely restricted to bracken and scrub. Here the ground cover would be expected to show the greatest resistance to Carabid movement, and the occurrence of Abax in these areas implies effective habitat differences. This is confirmed by experiments on the dispersal of Nebria beyond the plot, which again indicated that N. brevicollis rarely penetrates into the bracken or scrub zones. It is possible that deep litter and a vigorous ground-layer growth acts as a barrier and is responsible for the distribution of this Nebria population.

In the litter and grass areas Nebria appears to be scarce in the latter; those grass area traps with the highest ground cover frequency, take few Nebria. Such traps are concentrated in the top right hand corner of the plot, and their low catches may be a result of the ground cover acting as a barrier to Nebria movement, or may be a reflection of the trend towards higher densities at the bottom of the slope. Again dispersal experiments favour the former. This suggests that the concentration of Nebria

at the bottom of the slope is in part at least due to the ground cover acting as a barrier higher up.

Within the litter area, litter depths go up 2.5 inches, but if figures 36 and 38 and 39 are compared there appears to be no relation between litter depth and density of Nebria. In the litter area therefore variation in Nebria density must be attributed to such factors as the number of food organisms present, or temperature or humidity properties of the habitat, whose investigation lies outside the scope of this work.

In 1960 the occurrence of callow adults was recorded and their distribution is shown in Appendix table 33 and figure 39. They were taken in small numbers but the distribution follows that of the mature adults.

b) Movement of Nebria within the beech litter plot.

In the autumn of 1959 a total of 355 marked Nebria were released divided among four occasions.

Release	Date	No.
1	28/9/59	100
2	7/10/59	60
3	15/10/59	150
4	28/10/59	45
		355

No individual marking was carried out. Recaptures are shown in table 43. Their distribution within the unmarked population indicates the rate and direction of dispersal over the area of the beech litter. This was further investigated in the autumn of 1960 when 144 N. brevicollis were marked individually and released in 11 batches varying from five to 40 in number

TABLE 43. *N. brevicollis*. Releases and recaptures Autumn 1959. Beech litter plot.

Date	Total catch	Releases 1 28/9 (100)	2 7/10 (60)	3 15/10 (150)	4 28/10 (45)
28/9	130	-			
2/10	98	34			
3/10	143	18		Recaptures	
5/10	174	14			
7/10	102	6			
11/10	158	7	9		
13/10	299	10	10		
15/10	208	11	4		
22/10	225	3	6	13	
24/10	193	9	4	14	
26/10	197	7	4	12	
28/10	10	1	2	0	
2/11	54	1	2	3	6
4/11	93	1	2	2	5
7/11	68	2	0	2	2
10/11	27	0	0	4	1
13/11	0	0	0	0	0

(28/10/59. Many traps flooded by heavy rain).

Total marked: 355.

Above includes 5 peripheral traps not belonging to the plot.

TABLE 44. N. brevicollis releases and recaptures. Autumn 1960. Beech litter plot.

Date	Total catch	Releases 1 22/9 (39)	2 24/9 (23)	3 26/9 (7)	4 28/9 (5)	5 30/9 (10)	6 3/10 (31)	7 5/10 (10)	8 7/10 (8)	9 18/10 (9)	10 20/10 (14)	11 24/10 (10)
24/9	32	8										
26/9	10	4	-									
28/9	7	1	1	-								
30/9	22	5	3	3	-							
3/10	82	20	12	3	3	5						
5/10	58	16	9	1	1	7	9					
7/10	46	13	6	2	1	5	9	-				
13/10	12	1	1	-	1	2	6	1	-			
15/10	12	4	1		1	1	1	-	-			
18/10	41	7	7	2	1	-	11	2	2			
20/10	43	7	2	1	3	2	2	6	6	2		
24/10	60	11	4	2	3	3	10	2	4	7	8	
31/10	37	4	4	-	-	-	8	1	-	5	4	4
7/11	49	8	8	-	-	1	14	3	3	3	3	2

Including 5 peripheral traps not belonging to the plot.

After each release all traps were left inverted to allow uninterrupted Carabid activity, and were replaced in the trapping position for two nights before the next visit. Towards the end of the experiment when catches were low trappin was extended to three nights.

Initially in the first release recaptures were the highest percentages in zone I, and the lowest furthest from the point of release in zone III. Dispersal was not complete until the ninth day after release. The second marked sample had dispersed four days after liberation.

In the first release 58% of the marked Nebria were recaptured during dispersal and in case their rate of movement was reduced by a high proportion of the population being immobilised in traps, recapturing the third sample was delayed until the sixth day after release. However, the period required for achieving random distribution among the population was again eight to nine days.

In the fourth release the percentage of marked Nebria in the three zones fluctuated widely but once more less than 10 days seemed necessary for dispersal. During these last two releases catches declined and a single recapture constituted a correspondingly large percentage of the total catch. However, the rate of dispersal is of the same order as in the first two releases.

Recaptures can be used to estimate the absolute numbers of Nebria only after dispersal among the whole population; that is on or after:

Release	Date
1	11/10/59
2	11/10/59
3	24/10/59
4	4/11/59

In 1960, in order to ensure complete dispersal, it was presumed that 10 days were required by each release.

The 1959 recaptures establish that 5-10 days are required to disperse over the 2000 sq. yds. of the beech litter plot, and is similar to the rate which would be expected from the preliminary dispersal experiments described in section CI.

The same 1959 releases also indicate the direction of dispersal. Both the grid and the whole area studied can be divided into four sectors centred on the point of release (fig.4I) and the incidence of marked Nebria in each can be compared during and after dispersal. For this purpose all releases are considered together.

If, after dispersal, marked Nebria are distributed at random within the original populaion it is to be expected that they will constitute the same proportion of the total catch in each sector. The expected catch of marked individuals in each will be the same ratio to the observed total catch per sector as total recaptures are to total catch in the whole area. The significance of the differences between observed and expected catches of marked Nebria are compared for each sector (Table 45):

a) Whole area,after dispersal.

b) Grid only, after dispersal.

c) Grid only, during dispersal.

After the dispersal period, in the grid, and in the whole area, differences between observed and expected catch can be attributed to chance. This confirms that marked samples become dispersed over the whole area both as regards direction and distance from the point of release.

TABLE 45. Distribution of marked *Nebria* in 4 sectors of beech litter plot. Autumn 1959.

O = Observed marked catch. E = Expected marked catch.

(a) Whole area, after dispersal.

Sector	1	2	3	4
Total catch	189	140	698	417
O	57	27	170	97
E	46	34	170	101
$\chi^2(1)$	2.63	1.44	0	0.16
P	> 0.10	> 0.20	> 1.0	> 0.80

(b) Grid only, after dispersal.

Sector	1	2	3	4
Total catch	126	103	142	191
O	38	23	29	56
E	33	27	37	50
$\chi^2(1)$	0.76	0.59	1.73	0.72
P	> 0.30	> 0.30	> 0.10	> 0.30

(c) Grid only, during dispersal.

Sector	1	2	3	4
Total catch	126	116	152	189
O (M)	38	21	19	31
E	24	22	28	35
$\chi^2(1)$	6.00	0.05	2.89	0.46
P	< 0.02	> 0.80	> 0.05	> 0.30

However, within the grid during dispersal the proportion of marked Nebria is not the same in each sector. This is possibly the result of the position of the point of release within the beech litter area and the method of dispersal. The distribution of marked N. brevicollis at each side of the grid and at the top and bottom are compared in table 46 and related to the area of each sector including those parts lying beyond the grid. The total areas in sq. yds. are: - Sector 1 : 300, 2 : 200, 3 : 900, 4 : 600 (Figure 41). Sectors 1 and 2, and 3 and 4 are compared, and 2 and 3, and 1 and 4.

TABLE 46. Direction of movement of marked Nebria during dispersal. 1959. All releases.

Sectors	Total Catch	No. marked.	% marked	Area (sq. yds.)
1 and 2	242	59	24.4	500
3 and 4	341	50	14.7	1500
2 and 3	268	40	14.9	1100
1 and 4	315	69	21.9	900

This comparison is governed by the high catch of marked Nebria in sector 1, but it suggests an inverse relation between the proportion of the catched marked in each sector, and its total area. This implies that Nebria disperses radially, and probably explosively in all directions from the point of release, and in sectors 3 and 4 spreads over a large area. In 1 and 2, however, dispersal is soon stopped by the impassable, or unfavourable scrub and grass area, resulting in movement back to the litter. Later movement is reduced as marked individuals find suitable areas. Alternatively movement is at random after release and persists at the same rate after dispersal is complete.

These two possibilities were tested in 1960 when marking was carried out between 22/9/60 and 24/10/60. 144 individually marked Nebria were released in the centre of the 1960 grid near trap 25 (and hence also in the centre of the beech litter) and trapping was continued until 7/11/60.

Distances moved between release and, and between subsequent recaptures, and the time taken, are known; the mean distance moved per day is compared during and after the dispersal period in table 47. On the basis of the 1959 results this was taken to be 10 days. First recaptures made more than 10 days after release are not included in the comparison.

TABLE 47. Distances travelled by marked Nebria. Autumn 1960.

During dispersal.			After dispersal		
Recaptures	Days	Distance travelled. (yds.)	Recaptures	Days	Distance travelled. (yds.)
90	416	1670	152	1206	2615
Yds/day = 4.01			Yds/day = 2.17		

Ratio: Distance/ day during and after dispersal

$= 4.01/2.17 = 1.85$

During dispersal the amount of locomotor activity is therefore almost twice its level afterwards, and this supports the first suggestion, that there is explosive dispersal after release.

The direction of movement can be observed more easily in 1960 than in 1959 as the trap density was uniform over the whole area. The plot can again be divided in four sectors centred on the point of release (figure 42), and theirmarked catches during dispersal compared (Table 48). The area around traps common to two or more sectors is shown hatched in the figure.

A high proportion of the population was marked in 1960 and 'unmarked' in table 48 below includes both unmarked Nebria and recaptures of marked individuals after they had dispersed.

TABLE 48. Catches of 'marked' and 'unmarked' Nebria in 4 sectors of the beech litter plot. Autumn 1960.

Sector		1	2	3	4
Area (sq. yds.)		550	400	550	500
Excluding traps common to 2 or more sectors	Marked	18	3	13	13
	Unmarked	50	18	129	151
	% marked	36.0	16.7	10.1	8.6
Including common traps.	Marked	27	14	18	16
	Unmarked	105	86	210	219
	% marked	25.7	16.3	8.6	7.3

As in 1959 catches of dispersing Nebria were high in sector 1, but this is not an area effect as the release point was centrally situated and the four sectors were of very similar size. Further, the incidence of marked Nebria during dispersal cannot be related to total catch and there is no satisfactory explanation for it. It is noticeable that roughly the same proportion of dispersing Nebria were taken above and below the point of release in both years, that is in sectors 1 and 2 as compared with 3 and 4, (tables 46 and 48), if only the grids of 36 and 49 traps are considered. Most of the assymmetry can be ascribed to the distribution of marked individuals in sectors 1 and 2. Figures 41 and 42 show that the beech litter in sector 1 in both cases is in part bounded by grass, while all the others are limited by bracken or scrub. The association between grass and a litter layer less deep than that in bracken or scrub has been described in Section CII 1) and is illustrated by figures 35 and 36.

A possible explanation for the high dispersal catches in sector 1 is that Nebria reaching the limits of this area are not deflected by deep litter under scrub or bracken to other parts of the plot. However, this conflicts with the tentative hypothesis put forward with reference to table 46 above. Alternatively the reduced litter depth in sector 1 may allow more unimpeded horizontal movement and hence higher catches.

It has, however, been established that during the dispersal period of up to 10 days after release, marked Nebria show approximately twice as much locomotor activity as the rest of the population. This confirms the suggestion of explosive dispersal although it does not necessarily occur equally in all directions. A marked sample becomes dispersed over an area of 2,000 sq. yds. in not more than 10 days, and these results imply that the unmarked population becomes redistributed over the area every 15-20 days. This is to some extent confirmed by the pattern of recaptures; the movements of marked individuals selected at random from those taken five times or more after release, are shown in figure 43. These demonstrate the restriction of activity to the beech litter area, and that extensive movement about the plot occurs after the initial dispersal period.

However, capture, marking and release appears to stimulate activity, and capture and release alone may have a similar effect, thus exaggerating post-dispersal movement. On the other hand, the actual distances moved are underestimated by trapping, as the distance covered between captures will usually exceed that between the two traps concerned. It is perhaps legitimate to conclude that after dispersal locomotor activity declines but there is still considerable movement about the beech litter area.

2) c) Dispersal beyond the beech litter area.

Evidence on the rate of migration to and from the beech litter plot was obtained in two ways.

i) by trapping and marking Nebria in neighbouring beech litter areas and so determining the amount of exchange of individuals between them and the main plot.

ii) by studing the persistence of marked samples in the main plot, where extensive immigration would result in their forming a declining percentage of the total population.

i) There were two areas of litter near the main plot both of which were known to support populations of Nebria. The nearest part of the largest, i. the Rookery, was 80 yards from the centre of the plot. It lay to the south at the head of the Marsh and covered approximately 1200 sq. yds; the two areas were separated by bracken. Here 155 marked Nebria were released between 14/10/57 and 2/11/59. None was found in the main plot, and no marked individuals from the latter occurred in the Rookery.

The second beech litter area lay above the Wood Bank slope and its Carabid fauna has been described in the account of transect 2, (Section B II). It was separated from the main plot by 50 yards of scrub and grass and covered less than 100 sq. yds. The transect traps were visited 33 times between 28/9/59 and 13/11/59, daily after 12/10/59.

Here a certain number of marked Nebria from the main plot were trapped and formed 7.7% of the total catch (18 marked out of 233). This compared with 11.5% in the main beech litter area (236 out of 2049 Nebria trapped).

Catches in this transect are shown in table 49 and as far as possible are grouped in the same way as the main plot catches. In only one case, 15/10/59, were two individuals from the same release caught on the same day. Thus although in 1959 marking was by batches and not individuals, the figure of 18 recaptures may have been due to only 4 marked individual Nebria.

The number of marked individuals taken in the transect showed no appreciable cumulative increase with time. This, combined with a record of one individual from the second release occurring in the transect after one night of activity, suggested that movement to the the transect area occurred mainly during the initial disturbance dispersal period.

In the transect in 1959 the maximum possible number of recaptures was 2278, that is the sum of the numbers of marked individuals at risk each time the traps were visited, after releases had been corrected for mortality. This total of 2278 can be divided between possible recaptures during and after the 10-day disturbance dispersal period: respectively 832 and 1446. But on the main plot the traps were usually operated for two days at a time, immobilising each trapped Nebria for an average of one day. 236 recaptures were made and this number of possible recaptures was lost. 113 recaptures occurred during, and 123 after, dispersal. The corrected totals of possible recaptures are therefore:

During disturbance dispersal = 832 - 113 = 719.
After " " = 1446 - 123 = 1323.

Catches in the transect were distributed as in table 50.

TABLE 49. Catch of marked and unmarked Nebria in transect 2. Autumn 1959.

Date	Total catch	Marked recaptures Release 1	2	3	4
28/9	2				
5/10	3				
13/10	16	1	2		
15/10	23	1	3		
22/10	85	1		4	
24/10	6	-	-	-	
26/10	16	-	1	-	
28/10	12	-	-	-	
2/11	27	-	1	-	-
4/11	23	1	1	-	-
7/11	5	-	1	-	-
10/11	8	1	-	-	-
13/11	5	-	-	-	-
	233	5	9	4	-

TABLE 50. Catches of marked Nebria in transect 2 according to time after release. Autumn 1959.

Catches	Release 1	2	3	4	Total
During disturbance dispersal period	0	5	4	0	9
After " "	5	4	0	0	9
Total	5	9	4	0	18

If migration beyond the main plot occurred at a constant level after release it is to be expected that the distribution of recaptures in the transect would be proportionate to the respective numbers of possible recaptures. Thus the expected marked catch in the transect

during disturbance dispersal is:

$$18 \times \frac{719}{2042} = 6.3$$

this does not differ significantly from the observed value of nine:

$\chi^2 = 1$; $P => 0.30$.

In the previous section it was shown that during dispersal due to the disturbance of marking, the level of activity is approximately twice that afterwards; this effectively halves the maximum possible number of recaptures after disturbance dispersal relative to the number before. The expected number of recaptures in the transect during dispersal is thus raised to nine $(18 \times \frac{719}{1380})$. This is in fact the same as the observed number.

This analysis for 1959 therefore suggests that a high proportion of the emmigration from the beech litter plot takes place during the period of disturbance dispersal. The loss due to emmigration therefore lay between one and five per cent of the total population during the 1959 autumn activity, as it has been mentioned previously that between four and 17 individuals were trapped in the transect out of the 355 which had been marked in the main plot. In the small area of the transect the 4-17 marked Nebria probably included all those present.

It is probable that disturbance dispersal accounted for the majority of marked Nebria which reached the transect; but any other emmigration which occurred, without the stimulus of marking, was likely to be accompanied by some immigration.

Dispersal beyond the beech litter plot was also studied in the autumn of 1960 when attempts were made to determine whether a similar amount of emmigration occurred in all directions. The active population

was very much lower than in 1959 and as many Nebria as possible were marked, all individually; this necessitated a larger number of small releases.

54 traps were placed between 35 and 100 yds of the edge of the beech litter area grid, either in litter which supported populations of Nebria, or opposite each side of the grid, the nearest trap not closer than 35 yards.

(a) Transect 2) 11 traps of which the nearest was 50 yds from the edge of the grid.

(b) 3 traps in 100 sq. yds. of litter in an elm thicket. They were in the same group of trees as the transect and at the same distance from the grid, but 15 yds to the North.

(c) 10 traps in grass above the litter slope between it and the transect (a); traps were placed at random in a rectangle of 10 x 5 yds. parallel with the upper edge of the grid.

(d) 15 traps in bracken to the South of the grid between it and the Rookery; they were arranged at random in a square of 20 x 20 yds.

(e) 10 traps below the slope in bracken between the main plot and the Marsh, at random in a 10 x 5 yd. rectangle.

(f) 5 traps at random in scrub to the North of the grid.

The catches of each group of traps are shown in table 51 for the period 24/9/60 to 7/11/60.

The seven captures in the transect of marked Nebria from the main plot represent only four individuals. Of those marked specimens which were trapped beyond the main litter area the one taken in area (f)

TABLE 51. *Nebria* taken in traps near the 1960 beech litter plot.

	Areas					
	(a) (Transect)	(b)	(c)	(d)	(e)	(f)
Total *Nebria*	90	28	6	14	4	15
Marked from main plot	7	0	1	0	0	1
Marked from transect	26	0	0	0	0	0

subsequently reappeared in the litter in which it had been originally caught and released, as did one of the four taken in the transect.

In addition marked *Nebria*, all of which had been trapped in the transect, were released and recaptured there as in table 52.

TABLE 52. *Nebria* marked and recaptured in transect 2. Autumn 1960.

		Release		
Date	Total catch	1 28/9 (14)	2 30/9 (17)	3 5/10 (5)
29/9	25	4		
3/10	24	5	3	
5/10	8	2	2	
7/10	4	2	-	2
13/10	2	-	-	-
15/10	1	-	-	-
18/10	9	-	-	-
20/10	6	1	-	1
23/10	7	-	-	2
25/10	3	-	-	1
29/10	1	-	-	-
	90	15	5	6

Of the 36 marked Nebria released in the transect three were taken in the main plot respectively 6, 9 and 5 days after release.

Those traps which were not in litter areas took few Nebria and of these only 3% (2 out of 67) were marked; one of them later returned to the main plot. It has already been suggested that the scrub and bracken areas impede or inhibit movement of Nebria and these low captures and recaptures do not suggest extensive emmigration. Both recaptures occurred within 10 days of release.

Of the neighbouring litter areas it was shown in 1959 that there was no exchange between the main grid and the Rookery litter, and the same may be said for the elm litter above the slope. Nor was there any exchange between the latter area and the transect; no marked transect Nebria occurred there, and 10 marked individuals liberated in the elm litter in June 1960 were not trapped in the transect although several recaptures were made near the point of release. The elm litter was surrounded by a dense ground cover of elm saplings, nettles and Holcus which accounts for the absence of migration to and from it.

The transect therefore remains the only area in which appreciable numbers of marked Nebria from the main plot occurred. In 1960 144 marked individuals were released in the latter area and four reached the transect, while three out of 36 moved from the transect to the main plot. This suggests that about 4% (7/180) of the populations of the two areas are involved in exchange between them. But all the Nebria from the transect found in the grid travelled there within 10 days of release as did two of those from the main plot trapped in the transect. It is probable therefore that in the undisturbed population in the main plot the rate of emmigration

is less than the recaptures here suggest. This agrees very closely with the rate of loss in 1959.

ii) The second way of determining the amount of movement out of the beech litter area is to find the percentage of marked individuals in the population within the area itself. If migration occurs the percentage of marked Nebria in the population will fall.

The simplest approach is to plot the recaptures as a percentage of the total catch against days after release. This is done for 1959 in figure 44 (table 43, Appendix table 35).

The first two releases both show a rapid decline in the marked percentage for the first 10 days; after this the level fluctuates for about 20 days and finally falls. The initial high percentage coincides with the period of disturbance dispersal over the plot which has already been described. This therefore does not imply extensive emmigration, and this is supported by the rather constant marked percentage during the following two to three weeks. The final fall occurred when total catches were low and may or may not be significant. Catches were so low after heavy rain on 28/10/59 that the percentage figures for that day are not included in the figure.

In the third release the dispersal activity was not apparent, although it was shown by the fourth marked sample. (As in the analysis of dispersal within the plot here also one release is anomalous).

It might be suggested that there is a general downward trend in the percentage of marked individuals in the population in the case of the first two releases (Fig. 44) implying emmigration. However, this fall is probably apparent, not real. If all the releases and recaptures are corrected to

equal the same proportion of the population on the day of release, it is possible to eliminate bias due to the higher percentage of the population marked on some occasions than on others. This then allows direct comparison of the overall percentage of the population marked in each sample from the date of release until the end of observations.

The time over which any release was investigated varied from 13 to 43 days. In a corrected sample a steady loss of marked individuals due to migration would be shown by their recaptures forming a lower overall percentage of total catch in the earlier releases than in the later.

The total catch per day of the beech litter plot traps during the ten-day dispersal period is one indication of the active population, and in table 53 releases are corrected to equal the mean catch per day on the whole plot during the dispersal period.

TABLE 53. Autumn 1959 Beech litter plot releases corrected to equal initial catch/day.

Release	No. released	Initial Catch/day	Correction factor	Corrected release
1	100	$419/6 \simeq 70$	0.70	70
2	60	$665/6 \simeq 110$	1.83	110
3	150	$418/4 \simeq 105$	0.70	105
4	45	$1447/5 \simeq 30$	0.67	30

In this case releases are corrected to form a similar proportion of the total population by using pitfall catches, but it has been argued in an earlier section (A III), that owing to variations in activity non-simultaneous catches do not give a reliable indication of population density. An alternative is for the corrections to be based on the population

estimates from the following section, although these are dependant on the results described here. Table 54 shows the alternative correction where releases are corrected to equal $1/20$ of the estimated population on the day of release.

TABLE 54. Beech litter plot releases corrected to equal $1/20$ of the total population on the day of release.

Release	No. released.	Estimated population on day of release	Correction factor	Corrected release
1	100	2200	1.1	110
2	60	2200	1.8	110
3	150	2100	0.7	105
4	45	900	1.0	45

The overall percentages of marked individuals are compared in table 55. Catches within 10 days of the release date during disturbance dispersal are not included as it has been shown that activity is high during their initial period of dispersal and the level (and hence also the number of recaptures) appears to vary between releases.

TABLE 55. Marked individuals as a % of total catch after dispersal. Beech litter plot. Autumn 1959. Releases corrected from (a) pitfall catches (b) population estimates.

Release	Total catch	Total recaptures	Correction factor		Corrected recaptures		Corrected % marked	
			(a)	(b)	(a)	(b)	(a)	(b)
1	1532	57	0.7	1.1	39.9	62.3	2.6	4.1
2	867	20	1.8	1.8	36.6	36.0	4.2	4.2
3	449	23	0.7	0.7	16.1	16.1	3.6	3.6
4	95	3	0.7	1.0	2.0	3.0	2.1	3.2

The fact that the totals in the final column (corrected % marked) are similar, is a fortuitous result of the choice of correction factors, as by chance the mean catch per day usually approximates to $1/20$ of the total active population. The significant point here is that the variation within columns (a) and (b) is slight.

Both the correction factors used are of doubtful validity if considered alone, but together afford useful additional evidence that emmigration is slight, for if a significant amount of migration occurred it would be expected that the total catch would contain a higher percentage of marked individuals in the last two releases than in the first two. In fact by whichever method marked samples are corrected the overall percentage of marked Nebria is of the same order for all releases.

Releases and recaptures in the autumn of 1960 are shown in table 44, and recaptures are expressed as a percentage of total catch in appendix table 36. As releases were small the calculated percentages show considerable variation, and in figure 45 the running means of pairs of adjacent points are plotted against time after release. With such small numbers it is not possible to distinguish the different phases of dispersal as in 1959, but the general pattern is similar. Although recaptures showed a slight decline a high proportion of marked individuals persisted in the beech litter area.

Appendix table 37 and figure 46 show the percentage of the total catch, and presumably population, which was found to be marked on each visit to the plot. They show that for the first 15-16 days the proportion marked rose to almost 80%. After this it fluctuated about a mean of 82%, and it is concluded that during this period the rate of emmigration

equalled the rate of addition of new marked individuals. After 7/10/60 33 further Nebria were marked and there was therefore a loss through dispersal beyond the plot of 33 marked Nebria in 30 days, or approximately one per day. The size of the population during this period is discussed in the following section, and the emmigration rate in 1960 was evidently similar to that of the previous year.

From the sum of these observations one can conclude that migration to and from the main beech litter area is negligible except towards the transect. This is possibly related to the absence of a deep litter, or a scrub or bracken barrier in places in the upper part of the main area, and to the large numbers of marked individuals taken in sector 1) (see section b)). The presence of one marked individual from the grid in area (f) might suggest that dispersal beyond the plot occurs equally in all directions, and in most marked Nebria do not find a suitable environment in which to settle. They therefore continue to disperse, while those reaching the transect litter tend to remain there. But if up to 5% of the marked population disperse towards the transect, equal dispersal in all other directions would involve a loss of, say, between 20% and 40% of marked samples and this is not in agreement with figures 44 and 45.

The greatest amourt of movement shown on any occasion was on 8/10/59 when an individual from the second 1959 release appeared 80 yds from the point of release after only one night of activity. But observations on pp. 147 and 158 onwards, suggest that the amount of movement in an undisturbed population rarely approaches this level. Therefore in the following section migration has been assumed to be negligible for the purpose of estimating population densities.

d) Autumn population densities.

Populations of Nebria in the beech litter area were estimated by marking and recapture in the autumns of 1959 and 1960. Releases and recaptures are shown in tables 43 and 44. In many ways the population studied was ideal for the application of marking/recapture techniques, as it has been shown that migration from the area was slight; in addition adults of this species emerge in the spring, and during the autumn numbers decrease. It can be assumed that mortality affects marked and unmarked individuals alike and therefore with a falling population and no migration or emergence, successive recaptures give successive estimates of the population on the day of release. For the means of these populations the variance can be calculated. Any increase in active population is revealed and by this method and subsequent recaptures give estimates of the maximum.

First the sex ration in the population must be considered as any change in the ratio combined with differences in the activity of the sexes may affect population estimates which depend on trapping.

The sex ratio during autumn 1960 on the beech litter plot and in adjacent areas is shown in table 56.

In no case is there any significant departure from the mean.

Estimates of the activity of each sex can be obtained (a) by calculating recaptures per marked individual released and, (b) from the number of yards moved per day after dispersal, (table 57).

TABLE 56. Sex ratio in N. brevicollis in traps. Beech litter plot and adjacent areas. Autumn 1960.

Date	♂♂	♀♀	Total	% ♂
22/9	22	17	39	56.4
24/9	14	9	23	60.9
26/9	9	4	13	69.2
28/9	8	7	15	53.3
30/9	17	12	29	58.6
3/10	50	32	82	61.0
5/10	35	26	61	57.4
7/10	34	13	47	72.3
13/10	7	5	12	58.3
15/10	7	6	13	53.8
18/10	28	19	47	59.6
20/10	37	9	46	80.4
24/10	36	25	61	59.0
31/10	22	16	38	57.9
7/11	30	13	43	68.8
Totals	356	213	569	Mean 62.6

TABLE 57. Activity of N. brevicollis ♂♂ and ♀♀. Autumn 1960. Beech litter plot.

		♂♂	♀♀
(a)	Released	90	54
	Recaptured	218	83
	Recaptures/Release	2.42	1.53
	♂/♀ ratio	1.58	1
(b)	Total distance between recaptures (yds.)	4112	1535
	Total days activity	1632	779
	Yds/day	2.53	1.97
	♂/♀ ratio	1.28	1

The mean of these male/female activity ratios is 1.43/1. This approximates rather closely to the male/female ratio in traps (1.67/1), which suggests that males and females are equally represented in the population. As there was no change in the proportions in traps, and hence also on the ground and in releases, throughout the autumn, the effect of changes in the sex ration on population estimates has not been considered further.

Population estimates were obtained by the Lincoln index with Bailey's (1952) modification for small numbers, and are shown in tables 58 and 59. No estimates were made during the disturbance dispersal periods of 5-10 days as shown in Section b) for 1959 and of 10 days after each release in 1960. No estimates were possible when nil-recaptures occurred.

The two estimates of 4700 on 4/11/59 (table 58) are clearly anomalous and have been ignored.

Trends in the populations are shown graphically in figures 47a and 47b, where estimates are plotted with a single standard deviation on each side. In 1960 estimates from the smallest releases of less than 9-10 are not reliable and are shown as open circles.

In both years the calculated populations are compatible with a steady fall in numbers from 2300 to 800 in 1959 and from 200 to 100 in 1960. In both cases mortality occurred at the rate of 1-2% per day.

In 1959 and 1960 there was an apparent increase in population in mid- or early October. As it occurred in both years it is probably a real increase in active population, due to the renewal of activity in diapausing Nebria being spread out over late September and early October. If this is so, the marked samples liberated before the maxima, give estimates of

TABLE 58. Estimated populations. Autumn 1959. Beech litter area.

Date of recaptures.	Releases 1 28/9	2 7/10	3 15/10	4 28/10
11/10	1987	954		
13/10	2727	1636		
15/10	1742	2508		
22/10	2511	1929		
24/10	1940	2328	1940	
26/10	2475	2376	2285	
2/11	2750	1100	2060	
4/11	(4700)	1880	(4700)	705
7/11	2300	-	3400	1035
10/11	-	-	840	630
Mean	2304	1839	2105	790
Variance	142,684	336,484	834,725	46,425
S.D.	378	580	914	215

TABLE 59. Estimated populations. Autum 1960. Beech litter area.

Date of recaptures	Release 1) 22/9	2) 24/9	3) 26/9	4) 28/9	5) 30/9	6) 3/10	7) 5/10	8) 7/10	9) 18/10	10) 20/10	11) 24/10
3/10	154										
5/10	135	136									
7/10	131	154	47								
13/10	253	150	-	32	43						
15/10	101	149	-	33	65	201					
18/10	205	120	98	105	[illegible]	108	140	112			
20/10	214	337	150	56	147	455	63	50			
24/10	198	281	142	79	152	172	203	98			
31/10	296	175	-	-	-	131	190	-	57	106	
7/11	217	129	-	-	250	103	125	100	115	175	167
Mean	190	181	109	61	131	195	144	90	86	140	167
Variance	2613	5692	2245	977	6734	17659	3134	749	1682	2381	-
S.D.	60	75	47	31	82	133	56	27	41	49	-

of the maximum populations after 15/10/59 and 3/10/60, not the populations on their respective release dates. Thus in 1959 estimates from the first two releases from 15/10/59 onwards are of the maximum. On this basis mean populations are recalculated in table 60 below.

TABLE 60. Adjusted populations. Wood Bank. Autumn 1959.

Date	Population	Variance	S.D.
11/10	1470	533,545	730
13/10	2181	595,141	771
15/10	2139	350,689	592
28/10	790	46,425	215

Similarly in 1960 all estimates from the first six releases are of the active population on 3/10/60. Adjusted populations are shown in table 61, where estimates for 5 and 7/10/60 and 18 and 20/10/60 are pooled. Although 30/9/60 is the eighth day in the 10-day dispersal period of the first release it is probable that dispersal was largely completed by then, and a value for the population before the maximum can be obtained from recaptures on the 30th. Bailey (1952) is followed for the estimated variance:

$$\text{Population} = \frac{39 \times 23}{6}$$

$$= 149$$

$$\text{Variance} = 53,968$$

$$\text{S.D.} = 352$$

TABLE 61. Adjusted populations. Wood Bank. Autumn 1960.

Date	Population	Variance	S.D.
30/9	149	53,968	232
3/10	156	7,790	88
6/10	120	2,660	52
19/10	113	1,998	45

The alternative population trends and mean daily catches on the plot are shown in figures ~~46 and~~ 47a and b.

The total population on the plot can only fall during the autumn, but mean daily catches in the figures do show maxima about 13/10/59 and 3/10/60, and therefore either type of population trend can be correct. If the first it implies that the whole population is active early in the autumn but the general level of activity only increases slowly. The second suggests that emergence of adults from aestivation sites is gradual, but after emerging all attain maximum activity very rapidly.

These two alternatives may be examined more closely by relating catch, estimated population and activity in 1959. Attempts were made in 1960 to test each by comparing distances travelled per unit time (and hence activity), before, during and after the apparent maximum. Unfortunately this occurred a fortnight earlier than in the previous year and owing to the time taken by marked samples to disperse no such comparisons were possible.

Catch is proportional to the product of population and activity; thus an indication of the level of activity at any time in a population can be obtained by dividing catch by estimated numbers. This is done for 1959 in table 62 where 'Populations (a)' assume a constant mortality and '(b)' a sudden increase in active population with a constant level of activity. In figure 47a the population trends can be extrapolated after 28/10/59 and figures for numbers and activity derived (bracketed in table 62). Activity levels from populations (a) and (b) are shown in figure 48. For convenience activity levels are x 100.

Here on the first premise, (a), that the active population falls

TABLE 62. Catch, population and activity of N. brevicollis. Beech litter plot. Autumn 1959.

Date	Catch/day	Population (a)	Population (b)	Activity 100 x catch/pop. (a)	Activity 100 x catch/pop. (b)
3/10	71.5	2050		3.49	
5/10	87.0	1950		4.46	
7/10	51.0	1850		2.76	
11/10	79.0	1675	1470	4.72	5.37
13/10	149.5	1575	2200	9.49	6.80
15/10	104.	1500	2150	6.93	4.84
22/10	112.5	1050	1700	10.71	6.62
24/10	96.5	950	1500	10.16	6.43
26/10	92.5	875	1200	10.57	7.71
28/10	35.0	790	1000	4.43	3.50
2/11	27.0	(550)	(800)	(4.91)	(3.38)
4/11	46.5	(450)	(700)	(10.33)	(6.64)
7/11	22.7	(300)	(600)	(7.57)	(3.78)
10/11	12.0	(150)	(550)	(8.00)	(2.18)
13/11	2.7	(50)	(500)	(5.40)	(0.54)

TABLE 63. Populations (b) calculated from mean activity level and observed catch. Autumn 1959.

Date	Population	Date	Population
3/10	1212	26/10	1568
5/10	1475	28/10	593
7/10	864	2/11	478
11/10	1334	4/11	788
13/10	2534	7/11	463
15/10	1763	10/11	203
22/10	1907	13/11	46
24/10	1636		

steadily throughout the autumn, the initial trend of activity is upwards, and after 13/10/59 fluctuates. The same procedure with the second type of population trend, (b), results in a fluctuating level showing a slight decline. If it is assumed that activity remains constant throughout the autumn in those Nebria which are active, populations (b) can be recalculated and estimates made for the periods before 13/10/59 and after 28/10/59.

In table 62 the mean activity (b) between these dates is 5.9 and new values for population can be obtained, for here:

$$\text{Population} = 100 \times \text{Catch}/\text{Activity}.$$

These populations are shown in table 63 and in figure 49; 2-point running means are plotted.

Carabid activity is favoured by high temperatures and humidities, and the products of temperature and humidity (means for trapping periods - Appendix table 38) are shown in figure 48. To some extent variation in activity can be related to weather; for example the high levels on 13/10/59 and 4/11/59, the drop from 28/10/59 to 2/11/59, and the final decline from 10 to 13/11/59. In figure 49 therefore the apparent fall in active population from 5/10/59 and the rise after 2/11/59 are weather effects.

Similarly in 1960 catches fell in mid-October during a cold period; (figure 47b), Mean grass minimum temperatures (Silwood screen) were:

1 - 10/10/59	46.5°F
11 - 18/10/59	32.5°F
19 - 31/10/59	41.0°F.

However, it has been mentioned that the early onset of maximum activity (or its suppression by low temperatures) did not allow any comparison of activity levels throughout the autumn. It was not therefore possible to

determine whether the whole Nebria population is active early in the autumn season, but at an initially low level, or whether emergence is soread over a period of some weeks with a uniformly high level of activity. But the maximum population in the litter area has been established at 2300 in 1959 and approximately 200 in 1960, and that the overall rate of mortality in both years, between late September and early November, was 1-2% of the population per day.

The problem of distinguishing between total population and active population also occurred when attempting to estimate the numbers involved in the spring emergence (section e)). Here there was some evidence that the activity level was constant and an increase in catch was due to an increase in the number of active individuals. This would therefore tend to support hypothesis (b) above.

e) Observations on larvae and callows.

Larvae and callows of N. brevicollis occurred in traps but their activity was less than that of the adults. The ratio of adult to immature catches is shown in table V Appendix 4. Whereas the work on adults so far described was concerned with the relatively simple state of a falling population with maximum activity, the larvae and callows present a more complex situation. Both emergence and disappearance occur and the latter does not necessarily imply mortality. Observations on larvae and callows may be related to conclusions reached from work on autumn adults.

Distribution. Capture of callows on the Wood Bank beech litter plot are included in figure 39 and appendix table 33 where the distribution does not differ from that of the mature adults.

Catches of adults, callows and larvae in the 23 traps from October 1958 to November 1960 are shown in table 64. The three traps on the Heath, Elm Hill and in Hill Copse are described on p. 92. Here the distribution of the immature stages corresponds closely with that of the adults although a rather large number of larvae were taken in grassland. Of these 28 occurred in three grass heath traps on Elm Hill beyond the sycamore litter trap and the heath limit of transect 2). In the account of this transect a high catch of Nebria in this part of the grass heath was noticed, and attributed to shade from the nearby Elm Hill woodland. The catches in these heath traps were: adults 41, larvae 28 and callows one; of the larvae 82% (25 out of the 28) occurred during the winter of 1958-59. This followed the wet season of 1958, (Appendix 4, Table II), and it has been suggested tentatively in Appendix 4, that in Carabidae a cool, damp breeding season allows either high fecundity or larval survival. The ratio of adult - immature stage catches, in the different habitats and the Elm Hill heath, may be compared (table 65).

TABLE 64. Catches of N. brevicollis stages in 23 traps according to vegetation type. 1958-60.

Vegetation type.	No. traps.	Total catch and catch/trap. Adults		Larvae		Callows	
Beech litter	8	2668	333.5	103	12.9	164	20.5
Bracken	3	180	60.0	5	1.7	7	2.3
Grass heath	9	134	14.9	36	4.0	1	0.4
The heath	1	20		7		1	
Elm Hill (Sycamore litter)	1	141		6		0	
Hill Copse	1	157		8		5	
Totals	23	3300		165		178	

TABLE 65. . Larvae and callow catches as % of adult catches in habitats.

Catch as % of adult catch	Beech litter	Bracken	Grass heath (less Elm Hill traps)	Elm Hill heath traps
Larvae	3.86	2.78	1.08	15.42
Callows	6.15	3.89	0	2.44

If only the typical litter, heath or bracken traps are considered the table implies that there is less successful breeding in bracken and grass heath than in beech litter, and that in litter a high proportion of larvae reach the callow stage. Trapping differences in the three types of ground cover must be remembered, but at least there is an evident grass heath - woodland difference in favour of the latter, in production or survival of the immature stages.

In the Elm Hill heath traps the catch of larvae is significantly higher than would be expected even if the adult - larva ratio was as in woodland (E = 16; O = 28; χ^2 = 8; P = <0.01). On the other hand it was suggested in section IV than an open habitat may be more favourable than the typical one for woodland species if they are not excluded by low humidities. However, it is also noticeable here that the proportion of callows following the larvae was very much lower than in woodland, suggesting high rates of larval or callow migration or mortality. Catches of callows and larvae show that, at least compared with the adults, they are relatively inactive, and this would confirm the suggestion of mortality which could be attributed to the effect of the dry season of 1959. In turn this supports the extension of Richards' (1960) theory to local populations; that is that at the limits of a distribution, here the edge of the Elm Hill woodland, colonisation will be permitted by a favourable season but subsequently the population of the newly invaded area will be particularly

susceptible to the effects of weather.

Dispersal. It has been mentioned that Nebria larvae are less active than the adults,and observations of Hamilton (1917), Kern (1921) and Tipton (1960) show that they are more liable to be restricted in their movements by the humidity of the habitat. Similarly the callows are relatively inactive, and neither stage is likely to effect significant dispersal.

Between 3/5/60 and 11/5/60 seven traps on cultivated ground in Hill Bottom took 22 N. brevicollis of which 18 were callow. It is not normally a species of arable land and this suggested some callow dispersal, especially as during the same period woodland traps took 42 of which only 22 were callow. However, the difference is not significant (E = 12; O = 18; $\chi^2 = 3$; P => 0.05), and the question of callow dispersal was not further investigated.

94 Nebria were marked and released in the beech litter area as shown in table 66 in the spring of 1960. Recaptures are shown below in table 66.

TABLE 66. Recaptures of N. brevicollis released, beech litter area, spring 1960.

Area	April	May	June	July	August	September
Beech litter plot	2	13	3	-	-	19
Transect 2)	-	1	-	-	-	2
Other areas	-	-	-	-	-	1

Those trapped in the autumn were remarked and subsequent captures are not included. The only area in which marked specimens were found, apart from the beech litter plot and transect, was bracken to the East of the main

plot. Here one was trapped at a distance of 45 yds from the point of release in September. Thus of 94 released four left the main plot, and three of these were not trapped until the autumn activity. This emmigration is of the same order as that already described, and again there is no evidence of dispersal activity during the spring emergence.

Spring population densities.

N. brevicollis were marked and released during the spring activity on the beech litter plot. From the recaptures made estimates can be obtained, of varying value, of the size of the overwintering population and the spring emergence. 94 N. brevicollis were released and releases and recaptures are shown in table 67.

TABLE 67. Releases, recaptures and estimated populations. N. brevicollis. Beech litter plot. Spring 1960. (See text below for explanation)

Release date.	No. released	Recapture date	No. recaptured	Total catch	Population	S.D.
15/4	10	24/4/60	2	10	36.7	14
		17/5/60	1	14	* 75.00	40
4/5	25	10-13/5/60	3	15	*100.0	26
		22-24/5/60	2	14	*125.0	56
11/5	14	17-20/5/60	5	23	*106.0	18
17/5	10	7- 9/6/60	2	12	* 43.3	23
20/5	11					
25/5	4	No spring recaptures				
30/5	4					
9/6	10	12/6/60	1	3	20.0	8
21/6						
28/6	6	No spring recaptures				
4/7						

*Mean of estimates 10-20/5/60 = 89. S.D. = 32.

In Appendix table 39 and figure 50 are shown the trends from March to July 1960 of total catches and the percentage of callows on the beech litter plot. This shows maximum catches and a peak of emergence on approximately May 14th. Therefore all population estimates about and after this date are of the maximum, indicated * in the figure.

Those before mid-April, that is before the appearance of the first callow, are of the overwintering population; there is a single estimate of 37 on 15/4/60. Some individuals were trapped which had been marked in the autumn of 1959; total catches before callow emergence were 18, and of these 4 (or 22%) had been marked in the previous year. This does not differ significantly from the number which could be expected on the basis of the percentage marked in the area in 1959 ($21/_{188}$ = 11%).

E = 2; O = 4; χ^2 = 2; P = > 0.10.

The estimated population during the maximum was 89 $\pm$ 64 (at the 5% level of probability); afterwards it declined as shown by the catches and the 9/6 /60 estimate. From 15/4/60 to the spring maximum in the middle of May 49 marked individuals were released (table 67). During and after the maximum (17-24/5/60), they yielded 11 recaptures in a total catch of 40; from this is obtained a population estimate of 167. This is near the upper limit of the probable range of the alternative estimate, and approximates to the size of the autumn maximum.

Recaptures of spring-marked Nebria in the autumn of 1960 are shown in table 68.

These recaptures give an estimate of the population when they were released in the spring, but the uncorrected estimates greatly exceed

TABLE 68. Captures of N. brevicollis, marked in spring 1960, in the autumn. Beech litter plot. (94 released).

Date	Total catch	Marked	Estimated population. No. mortality	Mortality in over-wintering individuals.
19-20/9	37	6	526.6	271.4
21-22/9	38	3	914.5	482.5
24-26/9	42	4	808.4	410.0
28-30/9	29	2	940.0	500.0
3- 5/10	140	8	1472.7	777.8

those of the previously calculated spring and autumn populations. However, the incidence of callows in the initial releases was as follows: release 1): $0/_{10}$; 2): $1/_{25}$; 3): $5/_{14}$; 4): $9/_{10}$. After this the first callows had become mature (p. 57). It is probable that in these earlier releases the mature individuals had overwintered as adults; there were 44, suggesting that most of those surviving the winter were marked in the spring. If it is assumed that none of these survives to enter a second autumn the total spring release becomes reduced to 50. (In fact only two of the 44 were trapped in the autumn experiments). The spring population is recalculated on this basis from the autumn recaptures in table 67.

This estimate is still twice the spring population obtained from other data; it may be a true value in which case there is heavy mortality in the summer months, but Tipton (1960) found very little during this period. Alternatively, it can be attributed to a combination of emmigration and loss of marks.

Estimation of the spring population raises the same problems of

activity as did the autumn but in a more acute form. Catches, and hence activity were low, although the number of Nebria present must at least have equalled the autumn maximum, which approached 200. This may be due to a generally low level of activity, to a relatively high level for a short period after which individuals retire to aestivation sites, or to part of the population not emerging until the autumn.

The discussion of Nebria diapause (p. 81) supports the last suggestion, but the number of recaptures implies that individuals are active for only a short time. By the end of May 88 marked Nebria had been released and from 23/5/60 to 19/6/60 recaptures constituted 10% of the total catch ($4/_{42}$). It might be assumed that by this time 100% mortality had occurred in marked individuals which had overwintered as adults which would reduce marked numbers to 44. Even so between 50% and 26% ($44/_{89}$ and $44/_{167}$) would be expected to be marked. The capture of four marked out of 42 is significantly lower than either of the percentages.

$E = 21;\ O = 4;\ \chi^2 = 11.0;\ P = < 0.001.$

$E = 11;\ O = 4;\ \chi^2 = 4.4\ \ P = < 0.05.$

From this one must conclude that those marked in the early part of the spring maximum had become inactive by the latter part of May and early June and that any individual is only active for a short period.

f) Aggregation.

Aggregation may occur at a number of different levels; in Section A II, (p. 9), instances of aggregation on a small scale are recorded in N. brevicollis, and at the other extreme the population of the beech litter area is a large scale aggregation. Between these levels the distribution of Nebria in traps within the Wood Bank population is aggregated. The catches of 10 traps chosen at random from those of the 1960 grid in the litter area are shown in table 69.

TABLE 69. Catches of N. brevicollis in 10 random litter traps. Wood Bank 1960.

Trap	Catch	Trap	Catch
1	5	6	54
2	11	7	40
3	28	8	11
4	9	9	11
5	15	10	22
Total		206	
Mean		20.6	
Variance		248.3	

The ratio of variance to mean exceeds one and indicates an aggregated distribution:

$$\frac{248.3}{20.6} = 12.1$$

The significance of the difference between this ratio and unity may be tested by calculating t (Greig-Smith (1957)):

Where n(Number of traps) = 10

Standard deviation = $\sqrt{\left[\frac{2}{(n-1)}\right]} = 0.47$

$$t = \frac{\text{Variance: mean ratio} - 1}{\text{Standard deviation:}}$$

$$= \frac{12.1 - 1}{0.47} = 23.6$$

D.F. = 9. P = < 0.001.

The degree of aggregation in N. brevicollis catches is therefore significant.

Attempts were made in the laboratory to study the formation of small scale aggregations. A glass tank 12 x 12 x 24 inches was filled to a depth of 3 inches with slightly damp sand, the surface of which was levelled off. On this 10 identical pieces of card of 2 x 2 inches were arranged in two rows equidistant from each other and the sides of the tank, and were supported $\frac{1}{4}$ inch above the sand with pins at each corner. The tank was closed with a glass sheet and kept in an insectary whose light and temperature resembled woodland, (p. 113).

Experiments were carried out in which 10 Nebria were released in the tank and their distribution under the 10 available pieces of shelter observed after at least one night of activity. Food was placed at randon within the tank and neither hunger or satiation appeared to affect the degree of aggregation.

These experiments were carried out on three occasions starting on 12/5/60, 18/8/60 and 8/10/60 using callows, disturbed diapausing adults and mature active adults in each case. An equal sex ratio was maintained, and experimental beetles were changed at least once during experiments. In each case observations were continued for at least one week. Shelters were numbered, so that 5 and 10 occurred at the same end. Results for

the first five days of each series of observations are shown in table 70.

This shows distinct clumping with all types of imagines. Its significance is tested by comparing the maximum under any shelter with the mean per shelter. χ^2 is shown in table 70 and P does not exceed 0.01. Therefore this degree of aggregation cannot be attributed to chance. There were no differences in the behaviour of the three stages of adult Nebria tested.

It is noticeable that aggregations tended to form at the ends of the tank, that is under shelters 1 and 6, and 5 and 10. The activity of Nebria in the tank usually took the form of movement around the edge of the sand area, and therefore the chance of an individual coming to rest near those shelters in the corners was increased. The probability is corner shelters 8, and the others 6.

A total of 120 Nebria were found under corner shelters and this differs significantly from the expected number of 83 $(\frac{8}{14} \times 145)$ $\chi^2 = 43.9$; $P = < 0.001$.

There was no apparent gradient of temperature or light intensity in the tank but this was checked by an experiment between 12 and 18/8/60. A circular tank of 14 inches diameter was set up in a dark bay in the insectary. It was illuminated from directly above so that there was no variation in light intensity. This was arranged to give a 14 hour day in phase with external conditions. 0 - 110°C mercury thermometers at four points on the circumference of the tank showed no differences in sand or air temperatures. Seven shelters were provided and in a circular vessel in a uniform environment all stood an equal chance of harbouring any of the

TABLE 70. Aggregation of N. brevicollis in rectangular glass tank.

Shelter	Number of N. brevicollis														
	12/5/60					18/8/10					8/10/60				
1				4	9								1	5	
2				1			3	1						2	
3								2							
4						1						3			
5	9	10	7			7	5	5	9	10		5	8	1	3
6				3	1			1			9				1
7							2	1			1				
8															
9						1						1			
10	1		2			1			1			1		1	6
Outside shelter			1	2									1	1	
χ^2	64.0	81.0	37.2	10.2	64.0	36.0	16.0	16.0	64.0	81.0	64.0	16.0	50.4	16.8	25.0

seven Nebria which were added. Results are shown in table 71.

TABLE 71. Aggregation of N. brevicollis in circular glass tank.

Shelter	Number of N. brevicollis				
1				1	1
2		1	5		
3	6				
4	1		1	4	
5		6		1	
6				1	
7			1		6
χ^2	25	25	16	9	25

As in the previous experiment it was found that aggregations were formed and in each case the probability of their occurring by chance was less than 0.01.

Preliminary investigations were made into the possible reasons for the formation of aggregations.

In Section B III (pp. 116-117) experiments were described which showed that in both P. madidus and N. brevicollis a high density inhibited locomotor activity.

Between 18 and 21/10/60 the effect of sex was investigated. Nebria were confined to 3½ inch petri-dishes lined with white filter paper and provided with a shelter of black paper. Eight of each sex were distributed as in table 72 with a replicate for each combination. The experiment was maintained under insectary conditions and visited 15 times. Activity (movement on the surface of the white filter paper), was recorded and is shown in the table.

TABLE 72. Activity in male and female N. brevicollis 18-21/10/60.

Sexes present	♂	♂♂	♀	♀♀	♂	♂♀	♀
Total nos. active	26	53	25	59	16		24
No. of individuals	2	4	2	4	2		2
Mean per individual	13.0	13.25	12.5	14.75	8.0		12.0
Maximum possible per individual	15	15	15	15	15		15
% activity	86.7	88.3	83.3	98.3	53.3		80.0

This suggests that male activity is reduced by the presence of a female, although it is doubtful how much confidence can be placed in these results with only one replicate for each combination.

Time did not permit further work on aggregations, but it has been established that they are formed by N. brevicollis under uniform conditions, and it is possible to suggest a mechanism by which this occurs.

Allee (1926) concluded that in land isopods aggregations are formed "Primarily through tolerance of other individuals in a restricted favourable region". In N. brevicollis the tolerance is present although it is presumed that the laboratory environment is uniformly favourable. However, this species reacts negatively to light and is strongly thigmotactic. Thus at rest it is restricted to the shelters provided; here activity, and hence movement to other shelters, will be reduced in males by the presence of a female and in both sexes by a pre-existing aggregation. In an uninhabited shelter it may be supposed that movement is not arrested and continues until another Nebria is met.

However, information is still required on the relative importance to behaviour, of light, contact and the presence of other Nebria. In addition, it has been mentioned that density effects are not peculiar to Nebria, or indeed to aggregating Carabidae, although it is possible that in P. madidus and other less social species where aggregation is not recorded, there is mutual repulsion.

The greatest problems, however, arise in applying indications from these laboratory experiments to the field. In the latter the environment is far from uniform and beech litter offers abundant shelter, while in the laboratory the positive reactions of Nebria to darkness and contact are such that the more uniform the surroundings the greater the tendency to aggregate. On a white tray or paper N. brevicollis tends to come to rest against any dark object that is offered whether it is another free Nebria, a tethered or dead one, or a screw of black filter paper. To some extent this effect will obtain in the insectary experiments, increasing as experimental conditions become more uniform. The same problem is apparent in the results of work by Ellis (1953, 1956), and Ellis and Ashall (1957) who studied aggregation in locusts by methods similar to those used here, and in the field. The preliminary work described here and that of Ellis (1956) suggest that laboratory studies are most profitably carried out on a comparative basis with two or more species.

The advantage obtained from aggregation, and indeed its frequency in the field, is not clear. Observations in Section A (p. 10) suggest that in some cases it results from mutual tolerance and a scarcity of shelter, or a limited favourable area, but in others it may have some positive significance. Brachinus crepitans for which there are several

records of aggregation, protects itself from predators by an explosive discharge from the anal region, and this is certainly most effective when released by a number of individuals together. Many Carabidae produce a similar distasteful or irritant secretion, and that of C. problematicus for example is painful to the eyes and face at a distance of 9 inches. Thus aggregation in Nebria may be a protective device.

Allee (1926) found that in terrestrial isopods aggregations to some extent allowed immunity to variation in the moisture content of the environment. Similarly, in N. brevicollis with rather little control of its rate of water loss (Tipton 1960), excessive transpiration may be reduced in aggregation by the locally high humidity it will produce.

Alternatively, there may be a selective advantage in aggregation in such species as N. brevicollis where breeding activity is delayed for some months after adult emergence. In the low populations of the autumn of 1960 (approximately one Nebria per 10 sq. yds. of litter) aggregation may assist in keeping the sexes together until mating has taken place.

3) CONCLUSIONS.

This work on *N. brevicollis* has shown that the population studied was confined to an area of beech litter, and there was evidence that emmigration was slight and only occurred in one direction. This resulted in some exchange of individuals between the main litter area, and a smaller one 70 yds. away.

These conclusions are based on pitfall catches, and recaptures of marked samples, and it has been suggested that catches should not normally be used to compare population densities in any area in which there is variation in the type or depth of ground cover. Also the work on *Nebria* has shown that marking causes disturbance activity which is above the usual level, and it is possible that trapping and release alone has a similar effect.

With reference to the first point, that pitfalls do not give a true indication of density, there is evidence (p. 157) that on the beech litter plot they do show a true distribution. But as the main *Nebria* area was surrounded by deeper litter and a denser ground cover which would impede movement, there must remain the possibility that populations here may have been slightly underestimated.

If trapping had any effect on activity the amount of migration in an undisturbed population would be less than that recorded on Wood Bank. Therefore the *Nebria* population studied may have extended further into bracken and scrub areas, and in the undisturbed state there may have been less communication between one part and another. There is, however, no reason to question the general results of the work on this species.

C III. Pterostichus madidus.

1) Areas studied and introduction.

The life history, habitat and daily activity cycle of P. madidus are described and discussed in Section B. In the summer of 1960 two populations of this species were studied; one was on the Wood Bank beech litter plot whose vegetation, litter layer and Nebria population are discussed in the preceding section. The other was in a level area of grass heath on Elm Hill 40 yds to the south east of the beech litter grid of traps.

On the heath a system of 24 traps, each 10 yds. apart, was placed on 5/6/60, and on 10/7/60 it was extended to form a square of 36 traps. The distribution of the traps in relation to nearby woodland areas is shown in figure 51. The floral composition of the heath was as described on pp 82-83. It was mapped by the same method as the Wood Bank plot (p. 150) but this revealed little vegetational pattern which was not apparent from visual inspection of the area. This consisted of an increase in the frequency of Holcus and Dactylis towards areas shaded by tree canopies. In addition the vegetation density was assessed subjectively in each quadrat. Attempts were made to determine cover by a point quadrat, but this was not practicable in the densest heath. Instead the vegetation was rated 0-5 according to the apparent resistance it would present to Carabids moving at ground level, where bare ground scored 0, and the deepest grass cover 5. In partial shade the Holcus became doninant and on the heath edges of these areas Conopodium occurred.

The heath plot was bounded to the North by the Elm Hill woodland (beech, oak, elm and bramble) and to the West by a line of scrub with oak,

birch, hawthorn and bramble beyond which grass heath again occurred; here the plot fell slightly towards Elm Slope. To the South and East heath stretched for 40 yds before passing into an extensive mown area to the South-east and it was grazed by a sheep to the South (fig. 51)

Trapping and marking was carried out in the heath from 5/6/60 to 25/8/60, and from 28/6/60 to 25/8/60 in the beech litter plot, this period covering the summer adult maximum of P. madidus. Attempts were made to parallel the work on N. brevicollis and experiments were designed on the basis of catches made in 1959. However in 1960 catches only reached a third of the 1959 level (478 in 1960 as opposed to 1472 in the same 23 traps in the previous year) (Appendix 4, Table I); thus the number of recaptures of marked individuals which were made was even lower than was expected from observations recorded in section C I 2), and very few conclusions can be drawn directly from the work on P. madidus. It is, however, possible to make comparisons with the Nebria results and indeed it is the contrast between the low level of recapture in P. madidus and the relatively high one in N. brevicollis that best illustrates the differences between the two types of population distribution.

It has been shown that P. madidus is a generally distributed species at Silwood with slightly higher catches being made in grass heath than in beech litter (table 19, p.91). The two plots in which the species was studied were in the same part of the Field Station and could be assumed to be subject to the same macroclimate, but sampled different vegetation types. They were placed close together in an attempt to determine the amount and direction of any migration from woodland to grassland; this is relevant to Williams' (1959(b)) argument concerning the establishment

of diurnal rhythms in P. madidus as it presumes that the typical habitat of the species is woodland (p. 122).

As in N. brevicollis information on the density, distribution and movement was obtained from the catches of traps within each plot.

2) Results.

a) Distribution.

Catches of P. madidus are shown in tables 74 and 75 from 9/6/60 to 25/8/60 on the Heath, and between 23/6/60 and 25/8/60 on Wood Bank. The two plots are comparable for the period 12/7/60 to 25/8/60 during which all the heath plot traps were in position. The total catch of the heath traps was 794 or 22.1 per trap. On Wood Bank the total was 178 in 49 traps or 3.6 per trap.

Table 19 (p. 91) suggested that P. madidus was mainly a grassland species, and this is confirmed by these catches. Grassland presents far more resistance to Carabid movement than litter, and therefore higher catches in the former imply a real difference in absolute numbers.

The spatial patterns of catches within each plot are shown in Appendix table 33 and figure 52 for the beech litter plot, and Appendix table 41 and figure 53 for the Elm Hill heath. Catches are from 3/5/60 to 25/11/60 in the woodland, and from 25/7/60 to 15/9/60 on the heath.

In the beech litter plot catches indicate a general distribution which bears no apparent relation to types of ground cover or litter depths.

The mean catch per trap during this period was 4.6 and the amount of variation was rather slight; three traps took none of this species, and the highest catch was 18. It is noticeable that this distribution is in contrast to those of N. brevicollis (Section C II) and Abax (C III) which are centred respectively on bare litter and bracken or scrub.

Similarly on the heath P. madidus was generally distributed over the whole area, but here differences in the catches of traps can be related to the types of heath in which they are situated.

Figure 53 shows that the higher catches fell furthest from woodland or canopied areas, that is towards the bottom and right hand side of the grid in the figure.

The traps were numbered as shown in figure 51 where 6, 7, 18,..... occurred on the right hand edge of the plot and comparison of Appendix tables 40 (frequency of certain plant species), and 41 (catches of traps suggests that the higher catches are associated with low vegetation densities; the Appendix table data are condensed in table 72.

Table 72. Vegetation density and catch of P. madidus. Elm Hill heath 1960.

Vegetation density	No. of traps.	Mean catch
3.0 - 3.4	8	29.0
3.5 - 3.9	12	31.8
4.0 - 4.4	8	20.75
4.5 - 4.9	8	20.0

This suggests that the catches of traps in different parts of the heath plot are determined by the resistance to movement of the surrounding vegetation and not by variation in numbers of P. madidus. However, high vegetation densities were associated with a high Holcus frequency, and it

has been mentioned that Holcus was most frequent under shade on the Elm Hill plot, that is on the Northern or Elm Hill woodland side of the plot and under the isolated oak (fig. 51); in these areas the majority of traps with a 100% Holcus frequency were situated (Appendix table 40).

In table 73 Holcus frequency is related to catch of P. madidus, vegetation density and the frequency of selected heath plants. It has been mentioned elsewhere (p. 83 and in Appendix 4) that Holcus although frequent in the open heath, is successful in partial shade, and on the Elm Hill plot true heath was characterised by a decrease in the frequency of Holcus and an increase in the incidence of other heath species. Of the latter Galium hercynicum Weigel, Lotus corniculatus L. and Stellaria graminea L., were selected to distinguish Holcus grassland and heath, as they show a loose spreading growth form, occurred amongst other species, and were frequently recorded in the quadrat used for sampling. Equally typical but more erect forms such as Hieraceum, Rumex or grass species were less frequently detected by this method.

TABLE 73. P. madidus catch and type of heath. Elm Hill plot 1960.

No. traps.	Holcus frequency.	Mean frequency selected heath spp.	Mean vegetation density.	Mean catch P. madidus.
4	6	4.5	3.5	58.7
5	6	3.8	3.7	31.0
7	7	3.4	3.6	19.1
6	8	3.8	3.8	18.0
4	9	2.0	4.2	15.0
10	10	1.7	4.3	24.7

This shows again that the relation between catch of P. madidus and vegetation density is inverse, and the relation between the catch and the trend towards tue heath is direct.

There are, therefore, three possible explanations for the distribution of P. madidus catches in the heath plot:

i) Differences in catch are determined by vegetation density, and do not reflect any variation in number of P. madidus.

ii) Catches indicate a high population in the true heath areas.

iii) In the true heath the relatively low vegetation density allows a higher degree of insolation at ground level which results in higher temperatures, greater activity and an increased catch.

Although it is almost certain that both the first and last factors have some effect, there is evidence to suggest that the second is the major factor. It has been argued that the catches of the heath and woodland plots reflect a real difference in population densities, and this implies that grassland is the more favourable habitat for P. madidus. In agreement with this it can be suggested that on the Elm Hill plot the absolute numbers increase as more extreme grassland conditions are reached, that is in the true heath, as compared with the woodland edge Holcus areas.

This is confirmed by the distribution of larvae of P. madidus; during this work a total of 20 have been taken, some in pitfall traps but the majority in hand collections. Of these two occurred in litter areas, three in bracken or scrub, one on cultivated ground and the remaining 14 in grass heath.

b) Population density.

Releases and catches in tables 74 and 75 show a very low recapture rate, as was expected from preliminary experiments with the species (pp. 144-147). Below, attempts are made to estimate from these recaptures, rate of dispersal and population density, but they are so low that few valid conclusions can be drawn from them and their chief interest lies in contrasting them with those in the spatially restricted population of N. brevicollis.

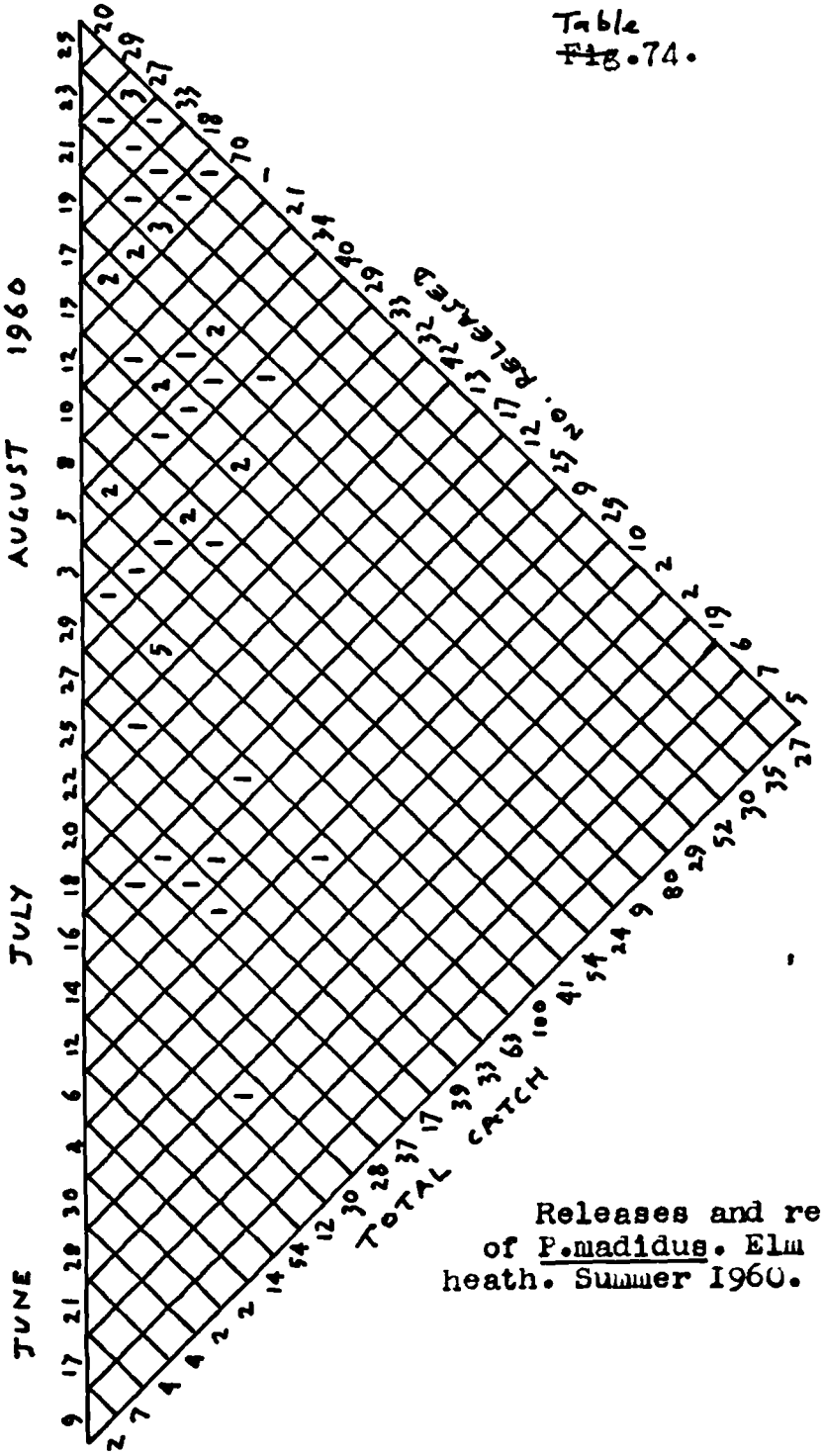
Attention is concentrated on the heath plot where the larger number of recaptures occurred.

First a general idea can be obtained of trends in the active population in the summer of 1960 from catches which are shown in Appendix table 42 and figure 54. In the figure a two-point running mean suggests a rather constant population from mid-July to the beginning of September assuming no marked changes in activity. This steady population may result from slight amounts of emergence and of mortality, or emergence exactly equalling loss due to death; the lack of change in the sex ratio in traps during this period (figure 10) supports the former.

Estimates of population density may be obtained from the recapture data by three methods, but are subject to considerable error.

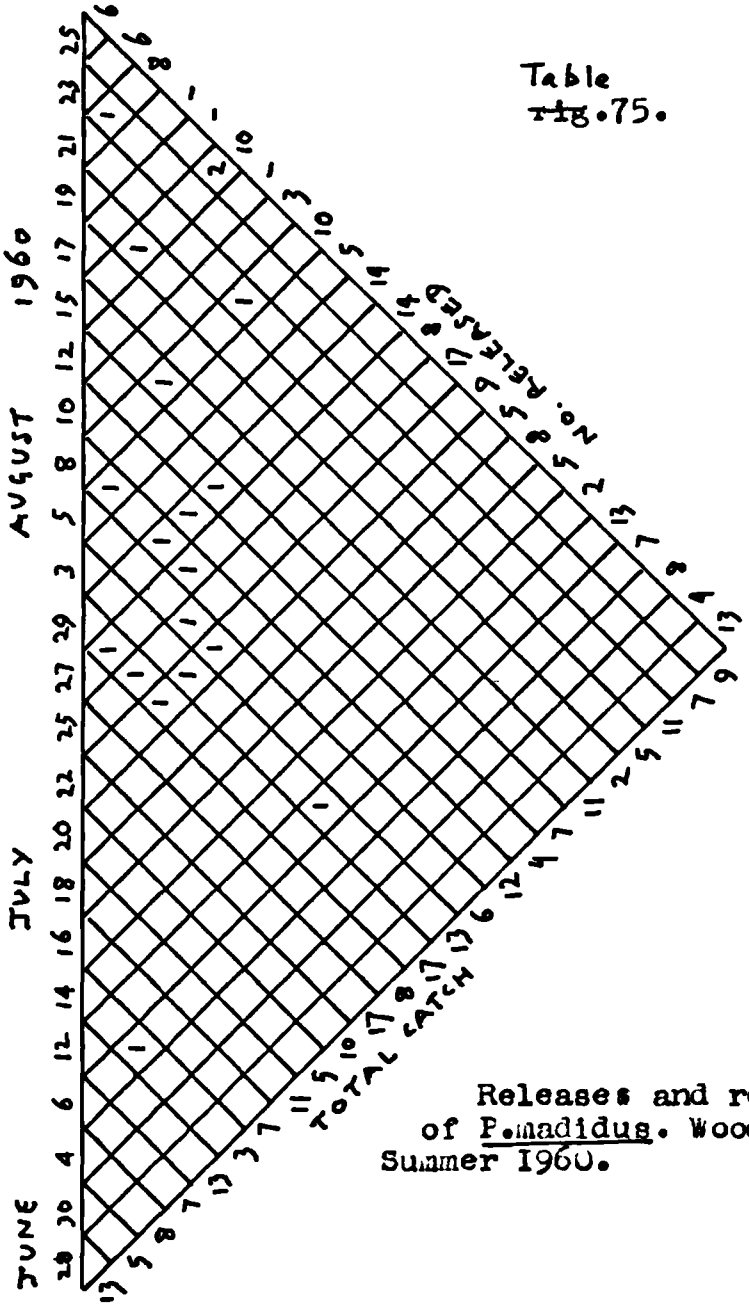
i) Nil-recaptures may be eliminated by pooling the information in table 75 to form six releases between 27/7/60 and 25/8/60, as in table 76. The intervals between median release and recapture dates range from four to seven days.

Table
~~Fig~~.74.



Releases and recaptures of P.madidus. Elm Hill heath. Summer 1960.

Table
~~Fig~~.75.



Releases and recaptures of P.madidus. Wood Bank Summer 1960.

TABLE 76. Releases and recaptures of P. madidus Heath plot, in 6 release and recapture periods.

Catches Dates	Total catch	Releases 27-29/7	3-5/8	8-10/8	15-17/8	19-21/8	23-25/8	Dates
		55	69	55	88	60	49	No. released
27-29/7	96							
3-5/8	141	2						Recaptures
8-10/8	78	2	2					
15-17/8	109	2	2	4				
19-21/8	82	0	0	2	6			
23-25/8	62	0	0	0	3	6		

This trellis can be analysed as a series of triple-catches, (Bailey 1952) to yield the following population estimates and variances (Table 77).

TABLE 77. 1960 P. madidus populations estimated by triple-catch method (from table 76).

Median date	Estimated population.	Variance	S.D.
4/8	2111	1,342,734	1159
9/8	579	106,211	326
16/8	553	168,846	411
20/8	305	48,032	219

ii) As with N. brevicollis a Lincoln index (with Bailey's (1952) correction for small numbers) may be used to obtain successive estimates of the population on the days on which releases were made. Table 75 shows that the majority of recaptures occurred within a fortnight of release, and no allowance is made for dispersal from the point of release, emmigration, or any increase in population. The estimates are shown in Table 78.

TABLE 78. 1960 P. madidus population estimates by Lincoln index.

Date	Mean population	No. of estimates
28/6	294	1
6/7	320	1
12/7	225	1
14/7	130	2
16/7	500	3
22/7	221	1
25/7	848	1
27/7	400	1
29/7	891	5
5/8	880	4
8/8	620	3
15/8	944	5
17/8	297	2
19/8	528	2
21/8	337	2

No correction is made here for the fact that up to 12/7/60 only 24 traps were in use, but it is doubtful to what area any of the estimates refer.

iii) In the following section it is assumed, as being the simplest possible case, that the population remains fairly constant during the period that catches only vary between 14 and 18 per day in the plot (fig. 54). On this basis it is calculated that a release of 100 P. madidus constitutes 6.6% of the total population after 0-4 days of activity, and all are dispersed out of the area after 20-24 days. Extrapolation of this trend shows that at 0 days after release they form 7.25% of the population; this is therefore:

$$\frac{100\ (100+1)}{7+1}$$

$$= 1224$$

$$S^2 = 293,500$$

$$S\ D = 542$$

There are considerable discrepancies between the population estimates arrived at in these three ways. The first involves fewest assumptions but the apparent trend in the four estimates bear little relation to observed catches. Conversely the second method gives estimates which agree far more closely with catches, but ignores population changes, and dispersal of marked samples. In the third type of estimate the premise that the population is constant does not agree with results of either of the other two methods. However, the mean population in August from the triple-catch analysis was 887, and by the Lincoln index, 601. Neither of these two figures lies beyond two standard deviations of 1224, that is the mean population estimate by the third method. It is most probable, therefore, that the maximum active population was present in August and either lay, or varied, between 600 and 1200.

Similar attempts may be made to determine the Wood Bank P. madidus; population but here only the Lincoln index method is available as only scattered, single, recaptures occurred. Catches and estimated populations for July and August 1960 form table 79.

As on the heath plot the trends in Lincoln index estimated populations agree with those in mean daily catches. This is illustrated in table 79 if mean catch per day, and mean population are compared in each period.

TABLE 79. Mean daily catch, and population on Wood Bank. July and August 1960.

Period	Dates	Catch	Days	Catch/ day	Mean Dates	Mean population	No. of estimates	Mean pop./ period.
10	July 3-16	33	12	2.75	6/7	14	1	52
					12/7	91	1	
11	July 17-30	60	12	5.0	22/7	58	3	68
					25/7	91	2	
					27/7	62	2	
					29/7	61	3	
12	July 31 - Aug.13	42	14	3.0	5/8	32	1	46
					8/8	60	2	
13	Aug.14 - 27	45	13	3.5	15/8	40	1	36
					21/8	32	1	

The relation between population estimates and catch may be compared for the two areas in August; during this month the best estimates are available for the heath; the population is taken to lie between 600 and 1200, that is 1000, and in table 80 populations of both areas are corrected to 3000 sq. yds.

TABLE 80. Catches and populations August 1960. Wood Bank and Elm Hill.

	Grass heath. Elm Hill.	Woodland Wood Bank
Population (in 3000 sq. yds.)	1200	34
Catch per trap	13.36	1.78

The relative levels of activity in the two areas are indicated by the catch/population ratio (x 100); they were:

Elm Hill - 1.1

Wood Bank- 5.2

This suggests a more active population in woodland; however, the Wood

Bank population estimates all depend on single recaptures and were calculated using Bailey's (1952) correction for small numbers, where :

$$\text{Population} = \frac{\text{number released} \times (\text{total catch} + 1)}{\text{number recaptured} + 1.}$$

On Wood Bank in August the total catch was large. (Mean = 6), relative to the single recaptures. As the numbers released were small the application of the correction for small numbers effectively halves the simple Lincoln index estimate. Without this correction therefore the estimated August population is approximately 68. The activity level on Wood Bank then becomes 2.6. Although this still exceeds the heath value it suggests that the estimated populations of the two areas are satisfactory, at least relative to each other. The higher level in the woodland may be only apparent and result from greater horizontal mobility, and hence more frequent trapping, in litter, as compared with dense heath.

c) Dispersal.

As in N. brevicollis the rate of loss of marked P. madidus indicates the amount of movement off the plot. If on the heath plot it is assumed that the population was the same size from mid-July, when the plot was extended, to the end of August as indicated by catches, and that mortality was slight, all releases during this period can be considered together. In Appendix table 43 and figure 55, recaptures are adjusted to each release equalling 100; they are expressed as a percentage of total catch for four-day periods after release.

This shows a steady fall in the marked percentage; if the trend is extrapolated a release of 100 constitutes 7.25% of the total catch, and

hence population on the day of release, and after 20 to 24 days forms 0% of the total. This corresponds to emmigration at the rate of 4-5% per day, and in a population of 1000 will equal 40 to 50 per day.

Migration was also investigated by trapping and marking beyond the heath plot. Four sets of traps were placed, one opposite each side of the main grid, within 35-40 yds. of its edge. They were:

1) to the South East, six traps in grass heath.

2) to the South West, six traps in grazed heath.

3) to the North West, six traps in grass heath below the belt of scrub on Elm Slope (see Section I).

4) to the North East, 10 traps in the Elm Hill woodland.

These were operated between 3/8/60 and 25/8/60 and their catches are shown in table 81 where they are compared with those of the main heath plot.

TABLE 81. Catches of P. madidus in peripheral traps and main plot. Elm Hill 3-25/8/60.

Traps	1	2	3	4	Main plot
Catch	54	28	8	4	381
Trap days	132	132	132	220	792
Catch/trap/day x 10	4.1	2.1	0.6	0.2	4.9
Marked catch (from main plot)	1	2	-	-	42
% Marked	1.9	7.1	0	0	11.0

None of the marked P. madidus released on Wood Bank occurred elsewhere and none of those from the heath plot was recaptured on Wood Bank.

Between 7/8/60 and 23/8/60, 30 distinctively marked P. madidus were liberated in the second group of peripheral traps, that is those to the South West of the main plot. Of these two were recaptured in the main plot in September after 31 and 41 days respectively. Another occurred 100 yards from the point of release after 38 days; it was taken in a trap in heath continuous with that investigated here, to the East of the Elm Hill woodland.

These recaptures, slight as they are, suggest that emmigration only took place in true heath; those traps in woodland or separated by it from the point of release, took no marked P. madidus. This is in agreement with the apparent distribution of the species in the area.

If only the traps in heath are considered table 81 shows a gradient in the percentage of the population marked, from the main plot (11%) to the traps 35-40 yds away (2-7%).

In the peripheral traps significantly less than 11% of the total catch had been marked and released in the main plot; catches of both sets of traps are combined, 11% of the total (82) is 9. The observed marked catch was 3 ($\chi^2 = 6$; $P = < 0.02$) and the difference is significan

This gradient may be related to the rate of loss from the main plot. Here dispersal out of an area of 2500 sq. yds. was complete after 20-24 days, and it is reasonable to suppose that at the middle of this period a marked sample most nearly approached general distribution over the whole plot.

If dispersal persists after 20-24 days at a similar rate it is possible to determine the time required to cover any given area. This

area will be in the shape of a sector of 90^{o} between South East and South West, for it has been suggested that movement only occurs in heath areas. The sector will be centred on the South West corner of the main plot, with a radius of 90 yds. (50 + 40 yds.), to include the two sets of peripheral traps. Its area is therefore 6,364 sq. yds., and it will take 28 days $\left(\frac{6364 \times 11 \text{ days}}{2500}\right)$, for a release to achieve the 50% dispersal level within it.

The peripheral traps were operated until 25/8/60 and cannot be expected to take marked P. madidus released within approximately 28 days of this date. The percentage of marked individuals in the traps should therefore be similar to the percentage in the main plot if those marked during August are excluded.

In the main plot 13 recaptures were made from 3-25/8/60, not including those released after the end of July, and they contributed 3.4% of the total catch. The expected captures of marked individuals in the two sets of peripheral traps as percentages of total catch are therefore:

Group 1) 3.4% of 54 = 2.

" 2) " " 28 = 1

1) and 2) combined - 3.4% of 82 = 3.

These do not differ significantly from the observed figures of 1, 2 and 3, respectively.

The observed recaptures are therefore consistent with a continuing rate of movement, over the heath area, similar to that observed during dispersal of marked samples from the main plot.

The low level of recaptures in P. madidus does not permit the

investigation of disturbance dispersal in releases, as in N. brevicollis. However, these observations suggest that the same rate of dispersal continues a month after release; thus disturbance in this case appears to have no effect.

It is of interest that there was no evidence of exchange of individuals between the heath plot and Wood Bank.

3) CONCLUSIONS.

Pitfall traps show that in the area of Elm Hill and Wood Bank catches of P. madidus were highest in grass heath, decreasing as the borders of woodland were approached and were lowest within woodland. A similar distribution with the highest catches in grassland was found in the 23 traps, although the difference was less marked. As the grassland-woodland transition is one of decreasing resistance to Carabid movement higher catches in the heath must represent higher populations. Therefore although P. madidus is generally distributed it can be regarded as primarily an inhabitant of grassland.

It was shown by Williams (1959(b)), and in the present work (p. 119), that in woodland P. madidus is nocturnal and in grassland, diurnal, in its activity. Williams' arguement on the establishment of these rhythms, (p. 22), requires this species to be typically an inhabitant of woodland with an inherent rhythm of nocturnal activity. At Silwood, however, it is a grassland species. It is a European species with a markedly western distribution, (Lindroth 1945), and there are no reliable records further East than Austria. It might be suggested that survival in open grassland habitats is only permitted in the more Atlantic climate of the British Isles, but Kirchner (1960) found P. madidus to be a dominant among Carabidae of cultivated ground in Germany. There is no evidence, therefore, to suppose that P. madidus is primarily a woodland species, at least with its present European distribution.

As in N. brevicollis, there is evidence that P. madidus showed extensive movement within the areas studied, although in both species it

is possible that this may be over-estimated owing to the disturbing effect of marking and trapping. P. madidus showed a much higher rate of dispersal out of the area covered by traps than did Nebria and this was due to its occurring in a continuously favourable habitat. In N. brevicollis in contrast any movement out of the area entailed entering or crossing unfavourable regions of scrub, bracken or grass. The difference between these two types of population is illustrated by the fact that in N. brevicollis where emmigration was slight, any increase in activity led to higher catches and recaptures. However, in P. madidus a higher level of activity would result in higher catches, but also in more rapid dispersal in a marked sample and thus in a reduction in the percentage of the catch which was marked.

IV OTHER SPECIES.

1) Calathus piceus.

It has been shown that this is a beech litter species (Section B II), with overwintering larvae and a summer adult maximum lasting from May until the end of August (B I).

C. piceus were trapped on the beech litter plot between 3/5/60 and 25/11/60; the distribution of catches is shown in figure 55 and Appendix table 33. This shows that, like N. brevicollis, it was closely confined to the litter area; comparison with figure 55 with 39 suggests that the two species differ in that N. brevicollis occurred in greatest numbers toward the bottom of the slope, while C. piceus was concentrated in the upper part. The C. piceus distribution bears no apparent relation to litter depth (figure 36), and the only environmental factors which can be invoked to explain it are shade and humidity.

In the litter area the shade intensity was least towards the bottom of the slope where two areas of grass occurred, (Holcus, Agrostis, Deschampsia and Festuca): the angle of the slope increased just beyond them and a change in drainage and soil moisture may have contributed to their presence. Thus humidity would have been highest under the blanketing effect of a closed canopy at the top of the slope, and least lower down, where the canopy was less developed, and the soil possibly drier.

It is possible that C. piceus is more dependant on a high humidity than Nebria, for table 19 shows it to be a more extreme woodland species. However, no information is available on spatial variation in the microclimate

of the beech litter plot nor comparative data on the water relations of the two species. In addition little is known of the habits of the larva of C. piceus.

Calathus trapped on Wood Bank were marked and released between 20/5/60 and 25/8/60; of 231 marked individuals 55 were recaptured.

To illustrate the order of size of the Wood Bank population, estimates from recaptures on 23/8/60 obtained by a Lincoln index with Bailey's (1952) correction are shown in table 81.

TABLE 81. Estimates of the population of C. piceus on Wood Bank. July-August 1960.

No. released	Date released	No. recaptured 23/8/60	Estimated pop. on day of release
8	27/7	1	76
7	5/8	1	66
8	8/8	2	71
5	19/8	1	42

This period covered the end of the summer maximum when numbers were declining , so these estimates must be of the populations on the days of release. They suggest a maximum population of less than 100.

During the last 10 days of observations on C. piceus, that is 15-25/8/60 marked individuals formed 28% of the total catch ($17/_{61}$). As 231 were marked in the area and the maximum population was less than half this figure, this implies extensive migration or mortality. The former is unlikely as the species is flightless at Silwood (p. 7), is apparently confined to the litter area, and no marked specimens occurred beyond the Wood Bank plot. Constant mortality is in agreement with

a long period of summer activity in this species, as the latter implies extended adult emergence; thus the absence of any pronounced late-summer build up of numbers can only be explained by mortality.

With emergence and mortality probably occurring at the same time in the population the scattered recaptures do not justify any attempt to estimate population levels throughout the summer.

2) Abax parallelopipedus.

Abax was trapped on Wood Bank from 3/5/60 to 25/11/60. During this period 271 adults were caught and 38 larvae; catches are shown in Appendix table 33 and the distribution of the adults in fig. 56. The figure illustrates the restriction of the adults to scrub and litter areas. The larvae were rather more widespread over the whole plot but their distribution closely followed that of the adults. Their catches in relation to adult frequency, are shown in table 82.

TABLE 82. Distribution of catch of larval Abax. Wood Bank 1960.

Adult Catch	0	1-10	11-20	> 20
No. of traps	6	36	5	2
Total larvae	3	27	4	4
Larvae per trap	0.5	0.75	0.8	2.0

Between 3/5/60 and 25/8/60, 256 Abax were marked and released on Wood Bank, but as the distribution of this species is obviously continuous with the other scrub and bracken areas along the slope, recaptures were necessarily low. 29 of the marked individuals were taken again, that is 11% of those released; this compares with 24% in Calathus piceus over roughly the same period ($55/_{231}$), and demonstrates the higher level of emmigration in Abax. Both species show an extended summer adult maximum and the total catches, (up to 25/8/60), were Abax: 270, Calathus: 246. Abax is the larger species and could be expected to show a higher rate of capture for any given population, but inhabited the area

with deepest litter which reduces catch. It is probable therefore that the maximum number present in the 3,600 sq. yds. of Wood Bank plot were similar to those of C. piceus, that is between 50 and 150.

It is not possible to confirm this tentative population estimate from marking and release data as recaptures were low. It has been suggested (p. 71) that Abax adults emerge throughout the summer and therefore extensive emmigration, mortality and emergence must occur together during the active season; this presents a situation too complex for analysis on the basis of the recorded recaptures.

Abax were also trapped in smaller numbers in the Elm Hill heath plot; catches are shown in Appendix table 44 and figure 57. Until 12/7/60 only 24 traps were in position and during this period Abax was only captured occasionally and is omitted from the Appendix table. Whereas figure 56 illustrates the distribution of Abax where scrub and bracken meet litter, figure 57 shows the pattern of distribution on a scrub-grassland boundary. Here the figure shows that this species only occurs on the edge of woodland and numbers are highest where there is scrub. The woodland to the North of the plot and to its left in figure 57 had an open grass-covered floor, and along its edge Abax was scarce. At the bottom of the plot, however, where scrub did occur, the majority of Abax catches were made.

These results confirm the conclusions reached in Section B II, from the catches of the 23 traps and especially from the two transects (pp. 96-99). That is that Abax, although occurring in beech litter and grassland, is essentially a species of scrub and bracken, which commonly occur between the two.

3) *Amara* species.

It has been shown (Section B II) that *A. lunicollis* and *A.communis* are species of grassland, and especially heath. Both species have an adult maximum rather early in the summer and in the Elm Hill heath plot the highest catches of both species were made in June and early July while only 24 traps were being used there. The maximum of *A. lunicollis* occurs rather later than in *A. communis*, and catches were made in the 36 traps. The trap distribution of these two species on Elm Hill is shown in Appendix table 57. The presence or absence of these species is related to vegetation in table 83:

(a) *A. communis* 2/6/60 - 12/7/60 (24 traps).

(b) *A. lunicollis* " " " "

(c) " " 13/7/60 - 25/8/60 (36 traps).

TABLE 83. Frequency of heath plant species (*Galium*, *Lotus*, *Stellaria*), for traps with, and without, *Amara* species.

		No. of traps	Heath plant spp. (3). Mean frequency per trap	*Galium* alone	Mean frequency per trap.
(a)	With *A. communis*	8	35	4.37	17	2.12
	Without	16	43	2.69	11	0.69
(b)	With *A. lunicollis*	20	73	3.65	26	1.30
	Without	4	5	1.25	1	0.25
(c)	With *A. lunicollis*	28	99	3153	35	1.25
	Without	8	10	1.25	4	0.5

In all these cases this shows a higher frequency of heath species

around those traps which took Amara. In addition there is a similar relationship between presence of Amara and frequency of Galium alone. In (a) and (b) at least this is closer than that between Amara presence and the three species together. The ratios of mean plant frequency with, and without, Amara can be compared: they are:

(a) three species 1.62 $(4.37/2.69)$; Galium alone 3.07 $(2.12/0.69)$.

(b) three species 2.92, $\frac{(3.65)}{(1.25)}$; Galium alone 5.20 $\frac{(1.30)}{(0.25)}$

(c) three species 2.82, $\frac{(3.53)}{(1.25)}$; Galium alone 2.50 $\frac{(1.25)}{(0.5\ )}$

It is possible this is the result of the total frequency of Galium alone being less than that of all three species combined, but it may be related to the actual distfibution of Amara species.

During direct quadrat sampling of Carabidae on the Elm Hill heath in July and August 1960, (see table 3 p. 18), 12 A. communis were taken and 9 A. lunicollis; the majority of both species were callow, and all occurred in or in soil below, Galium. Amara species tend to be phytophagous and this suggests that larvae of these two species feed on the tissues or seeds of Galium. If so, this explains the relative absence of the two species on arable land, where Galium does not normally occur at Silwood (tables 20 and 21; pp. 93-94). A number of Amara larvae were taken on Elm Hill both under Galium and other plant species, but it is only possible to identify them to the sub-genus Amara s.s. Of this sub-genus A. convexior, A. familiaris and A. aenea were recorded on Elm Hill as well as A. lunicollis and A. communis. Alternatively Galium may afford pupation sites for the heath Amara spp.

The fact that in (c) in table 83 A. lunicollis presence is relatively

less dependent on Galium alone may suggest that by the end of July considerable dispersal has been effected away from pupation sites into the heath generally.

Attempts were made to correlate the frequency of Amara lunicollis and heath plant species in the 36 traps. Amara catches were classed as 0, 1-5, 6-10, and 11-15. The corresponding mean plant frequencies were: three species - 1.25, 3.32, 4.60 and 3.25; Galium alone - 0.50, 1.32, 0.80 and 1.50. In neither case could a significant correlation be demonstrated; the values of r, the estimated correlation coefficient, which were obtained were respectively 0.68 and 0.69; for both P exceeded 0.10.

These observations show Amara lunicollis and A. communis to be heath species, and there are indications that their populations are centred on Galium. No marking was carried out to determine rates of movements or densities.

4) CONCLUSIONS.

Observations on these four species were made during more intensive work on *N. brevicollis* and *P. madidus*; they were selected as they were among the more abundant species after these two, and were frequently trapped.

C. piceus provides a further example of a population restricted to litter although there are indications that optimum conditions do not coincide completely with those which most favour *N. brevicollis*.

The distribution of *Abax* is of interest as it differs from that of either *P. madidus* or *Nebria*.

The two *Amara* species exemplify typical heath populations, but differ from the majority of heath species in that their distribution does not extend into cultivated ground as in such species as *H. rufipes* and *H. affinis*, *B. lampros* or *P. caerulescens*.

D. DISCUSSION.

Types of distribution.

In this work Carabidae were studied on the drier parts of the Field Station, in beechwood, bracken, grass heath and cultivated land. These vegetation types were selected for their uniformity and it was shown that they form part of a temporal succession. From the results of work on Carabid habitat it was concluded that their distributions were determined by the vegetation.

The Carabidae whose population distributions were selected for special study show a series according to habitat ranging from N. brevicollis and C. piceus in extreme woodland conditions, through Abax which was found in bracken and other vegetation on the edge of woods, to P. madidus which was generally distributed but most abundant in grassland, and Amara lunicollis and A. communis which were confined to heath.

The observed patterns of distribution may be compared with Elton's (1949) types described in the Introduction (p. 3). The reasons for these patterns may be considered, and they may be discussed in relation to the action of mortality factors.

Elton distinguished area and boundary patterns, which may be composed of centres of either periodic or inverse periodic distribution. Abax shows a boundary pattern and the other species area patterns. The periodic distribution of Abax is also to some extent inverse, as the typical bracken or scrub habitat occurs at Silwood between grassland and extreme woodland litter; both these types of ground cover are distributed periodically on a large scale and therefore the distribution of bracken or scrub, and hence also of Abax, show an inverse periodic distribution.

In defining the type of pattern in the other species problems of scale arise similar to those mentioned when the aggregation of Nebria was discussed (p. 195). For example in P. madidus grassland and woodland populations might be considered distinct, for there is no evidence of movement between the two habitats. Alternatively this species may be regarded as forming a single population on Wood Bank and Elm Hill as it is continuously distributed on heath and in woodland there and in neighbouring areas; in this case it can be maintained that it shows a large scale periodic distribution within the area pattern, in which the high densities occur in grassland.

In addition to such major spatial changes in density, minor variation also occurs as was demonstrated for N. brevicollis, (p. 195). The distributions of all the species (figs. 38, 39, 52, 53, 55) show differences in the catches of adjacent traps in apparently uniform parts of the habitat. It was argued (p. 156) that these differences were real effects of population density and did not reflect merely the efficiency of individual traps.

These distributions are therefore in agreement with Elton's suggestion that apparently continuous populations are divided among centres of relatively high density. It is also possible to distinguish between the typical area pattern and the boundary pattern of Abax, and it is suggested that this difference may be significant when possible mortality factors are considered.

However, within the species with area patterns there still remains a considerable range of distribution types. The population of Nebria which was studied, and also that of C. piceus in the same area, were typical gamodemes. In Nebria there was very little exchange with other areas, but

considerable mobility within the population. In P. madidus on the other hand, it appears that the continuity of a population, in the gamodeme sense, will only be interrupted naturally by such major barriers as lakes or rivers.

The two Amara species show an intermediate type of distribution as they seem to occur everywhere in grassland, at least at Silwood, and a population may cover an extensive area. However, it is probable that there will be little communication between different parts of such a large population, for although A. communis has been recorded as flying (p. 8), these species are relatively immobile when compared with N. brevicollis or P. madidus.

No definition of these types is attempted as they show a continuous range and are entirely dependant on vegetation. Thus in a larger area of beechwood, for example that forming Garden, Heath and South Lodge Woods, the pattern of distribution of Nebria approached that of P. madidus or Amara species. High Nebria densities occurred there (pp. 44-46), and the rate of dispersal of marked samples (p. 145) suggested movement over a wide area. Similarly there was evidence that small, isolated, open areas in woodland supported populations of grassland Carabidae (p. 99) and in flightless species there is unlikely to be much communication with other populations.

Causes of distributions.

While the type and extent of a population's distribution are determined by that of the vegetation, minor variation in density may occur according to properties of the different Carabid species or of the habitat. Local high density centres may result from spontaneous gregarious behaviour in the beetles themselves, as is possible in Nebria, or by aggregation about a food plant or pupation site, as can be tentatively suggested for Amara

species. In the other species these centres can be ascribed to variation in the microclimate, or the ground cover's resistance to movement.

Among the Carabidae studied there has been no indication of gamodemes occurring in continuously favourable habitats, apart from these minor centres of high density. This is to be expected for, with the possible exception of Amara species, all those whose population distributions were investigated, are to a large extent predatory and correspondingly active. Those which were marked were found to be capable of dispersing rapidly over wide areas.

Work on population distribution was confined to the commonest species, and this suggests that those studied possess a relatively high level of tolerance or adaptability. As they were also inhabitants of the most uniform and extensive types of vegetation it is inevitable that they should tend to show continuous area patterns of distribution.

In other, less abundant species, collecting has showed that where there is spatial variation in the basic soil type or in its water content, populations are more localised. For example it was found that Carabidae of damp places, which have not received quantitative study, were restricted to certain parts of low-lying or badly drained areas. The subjective impression gained was that distributions were determined by variation in soil moisture, humus content or shade. Similarly on the edge of arable land gradients of vegetation cover and insolation occurred. Here again patchily distributed populations were found often centred on shelter, and Thiele's (1960) work implies the presence of zonation in Carabidae according to the distance from hedge or headland.

It is therefore probable that continuous area patterns are the exception rather than the rule, and this is of interest if distribution in

populations is related to the possible effect of weather on numbers.

Distribution and density-independent factors.

The following discussion of the effects of climatic factors and distribution on density is based mainly on clonclusions reached with N. brevicollis, for in this species most work has been done on numbers and dispersal, and there is also some evidence for the direct effects of weather (p. 189, and Appendix 4).

It is a feature of the population distributions described here to show areas of high density and extensions at a lower density into other vegetation types, or in the case of Amara species, into other parts of the same basic vegetation types. This is true of adults and also of the larvae, where they have been found (that is in Nebria, P. madidus and Abax).

The presence of gradients in numbers necessarily implies gradients in the suitability of the habitat. The factors which may vary are the density of competitors, of predators or parasites, the food supply, the density of animals of the same species, or the physical properties of the habitat. Of these the last is likely to be the most important. It has been argued (p. 135) that neither enemies nor food will usually determine Carabid distributions, and here these are not considered further as possible factors. The effect of other individuals of the same species is discussed later.

There remain competition from other species and physical effects, and they may be considered together, as both probably act to confine species to their typical habitats. Of these the physical properties of the environment appear to be the most important. The role of temperature in determining activity levels in different habitats has been discussed

and reference has been made to the results of other workers on the water relations of Carabidae.

If Nebria alone is considered any movement from the typical litter habitat must occur, in the present context, in the direction of grassland. Here humidities will be lower, while higher temperatures will result in more rapid rates of metabolism and transpiration, and Tipton(1960) has demonstrated the susceptibility of Nebria adults and larvae to desiccation.

A general fall in catch, and in the case of Nebria a fall in population, in 1960, relative to 1959, is recorded (Appendix 4). It is tentatively attributed to the adverse effects of the dry summer of 1959 on survival and fecundity. On the basis of the present evidence this argument is speculative and is therefore relegated to the Appendix; it is, however, in agreement with Richards' (1960) suggestion that in insects the minor year to year fluctuations in numbers are caused by weather. This supposed action of low humidities on numbers can be related to distribution.

It was suggested (p. 136) that the temperatures reached in open habitats favour Carabidae from all the vegetation types studied here, but many species are normally excluded by low humidities. Any population colonising a habitat more open than the normal one, for example Nebria extending into grassland, will be particularly liable to suffer from a decline in the humidity of the new habitat.

For example, a grassland population of N. brevicollis on Elm Hill has been described (pp. 187-190), and there is evidence to suggest that migration into it was permitted by the wet season of 1958, but was balanced by considerable mortality in the following dry year. Movement in adult

Nebria is such that they are theoretically capable of returning to woodland should the grassland humidity fall, and on Elm Hill it seemed that the larvae were most affected. This conclusion is based on the argument in Appendix 4, and although the effect of weather on Carabid numbers has yet to be confirmed, it does provide the best explanation for these observations. A similar sequence of colonisation and extinction is liable to take place on the grassland boundaries of Abax populations.

This argument supports the thesis that variation in population density reflects the suitability of the environment, and any temporal change towards a less favourable state will result in greater extinction in peripheral areas than in the centre of the population. In fact this is Richards' argument applied on the scale of the local population or gamodeme, instead of that of geographical distribution. In fringe areas the lethal/or prohibitory level of any factor will be reached sooner than in the centre of the population, where conditions will be nearer the optimum, and in addition lower population densities chance will play a greater part in extinction or survival.

It is not known what factors limit the extension of Abax populations into litter, or restrict the density of P. madidus there, but it can be suggested that the same process will occur. However, it is unlikely that it will act to any significant extent between the minor high density centres within a population, (as suggested on p. 5) at least so far as the adults are concerned. It has been shown that marked variation in density occurs between traps in a favourable habitat, that is within a distance of 10 yds.. With the powers of movement which have been recorded in Carabidae, it is evident that on this scale they are capable of moving to the most favourable parts of the habitat. Larvae may be more affected but little is known of

their distribution, rates of movement, or physical tolerance.

The significance of the more linear distribution of Abax populations becomes apparent. This system of migration followed by an increase in adult mortality, or a fall in fecundity or larval survival, can only take place on the periphery of a population, and in the extensive type of area pattern the area in which it occurs will be small compared with that of the whole population. In Abax on the other hand peripheral zones occur on both sides of the distribution, and it is to be expected that the effects of climatic changes will be correspondingly increased.

It has been suggested that further investigation would show that in the majority of Silwood Carabidae extensive area patterns are exceptional, and that restricted distributions resembling the typical gamodeme would be found to predominate. This may even apply to other populations of the more abundant species; for example a probable breeding population of N. brevicollis was recorded under an isolated tree (p. 98). In such situations again the peripheral zone is large in relation to the total area occupied by a population.

Distribution and density-dependent factors.

If these supposed boundary effects do apply the intensity of their action will usually depend on the distribution of populations and not on their density. This is not to suggest that the density-independent action of weather is the main controlling factor in Carabid populations. Although it may account for annual fluctuations in numbers, a relatively steady state persists and this implies the operation of density-dependent controls, as maintained by Richards. There is evidence for this steady state in

that such common species as N. brevicollis, P. madidus and Abax tend to be the most abundant whatever the general level of Carabid populations (Table I, Appendix 4). The older hand-books such as those of Dawson (1854) and Fowler (1887) show that the frequency of the majority of the British Carabidae has changed very little in the last 50-100 years, and over a shorter period this has been confirmed by collecting since 1954.

Density-dependent factors will tend to operate most in the more densely populated central parts of a distribution; it is possible, however, that these effects will extend to the sparser populations of the fringe areas.

High densities within a population may set up pressure to disperse, leading to higher numbers in peripheral zones and a greater extension into atypical habitats; here migrant individuals will be particularly liable to the effects of weather whose action in this case will be dependent on density.

But it has been shown that high densities reduce activity in P. madidus and N. brevicollis (pp. 116-117), although experimental densities were artificially high. In Nebria, however, which forms aggregations, it is possible that denser populations in peripheral areas may mitigate climatic effects; the implication of preliminary work on aggregation in this species (pp. 195-202) was that isolation produces stress. Thus it could be suggested that in seasons of high density, on the edge of populations the company of other individuals may enhance performance, or more plausibly, that their presence will reduce activity and hence further immigration to areas which may be potentially even more unfavourable.

Conclusions.

Whatever the merits of these arguments it has been established that

Carabid populations extend at low densities into neighbouring habitats or vegetation types, where they may be more susceptible to adverse properties of the environment and to chance extinction. It has been suggested that weather may be important in this respect. It is probable that except in cases where major changes in the size of a population cause changes in its distribution, this effect will be independent of density. Such factors as weather will act at least in this way in populations with extensive area patterns, but such distributions appear to be exceptional among Silwood Carabidae.

It has not been the purpose of this discussion to develop any comprehensive theory of density control mechanisms, as the work with which it deals was primarily concerned with describing patterns of distribution and movement. It has shown, however, that distribution may well contribute to controlling numbers by influencing the severity of climatic effects. Work has been restricted to two-dimensional populations, but the importance of the peripheral area will be correspondingly greater in populations which occur in three dimensions.

Suggestions for further work.

Any extension of this work would require two different approaches which could be related subsequently to distribution. One is a study of the temperature and humidity properties of the different habitats, combined with work on the physical preferenda and tolerance of Carabid adults and larvae. The other is an investigation into factors which may be expected to control Carabid numbers in a density-dependent fashion, especially the incidence of predators and parasites.

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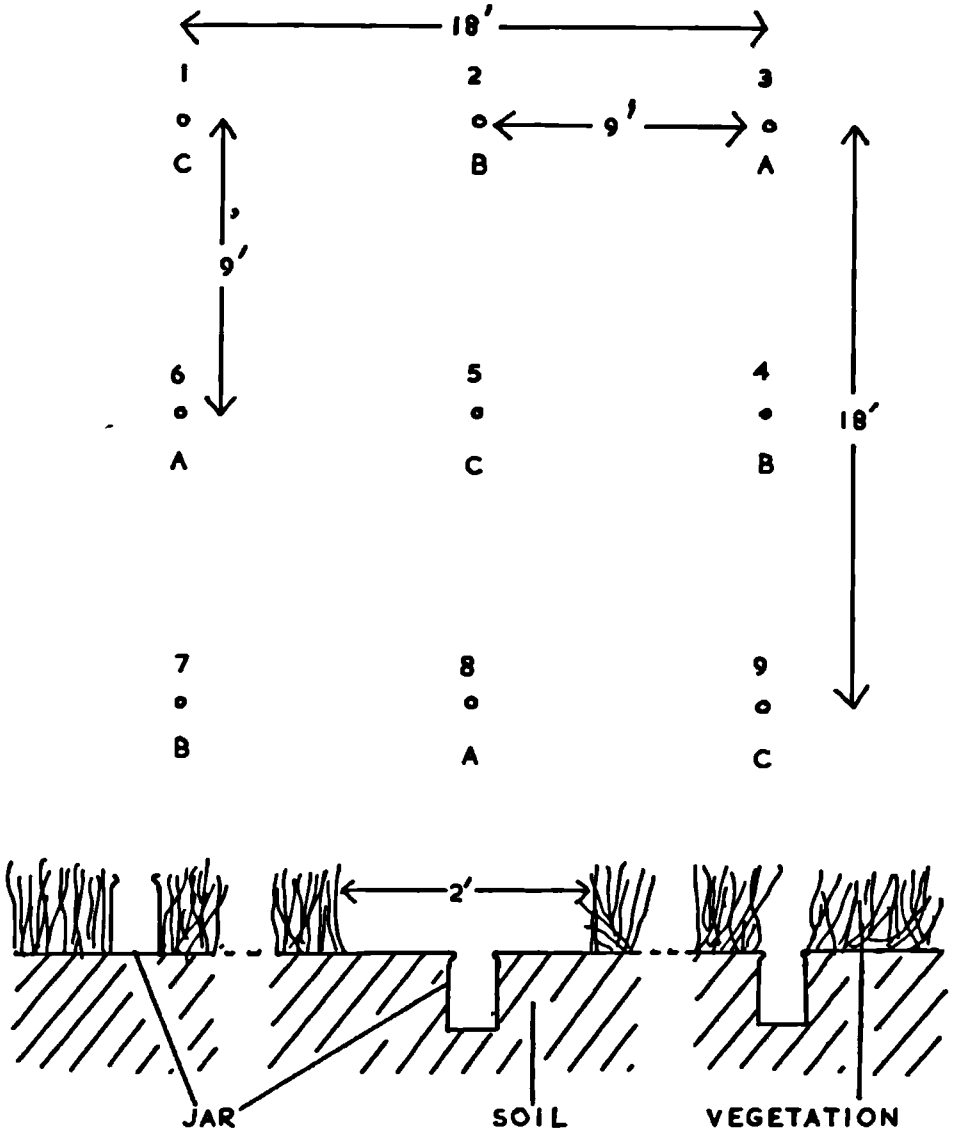


FIG. 1. ARRANGEMENT OF TRAPS IN PLOT 1., WHERE A, B, C, ARE TRAPS.

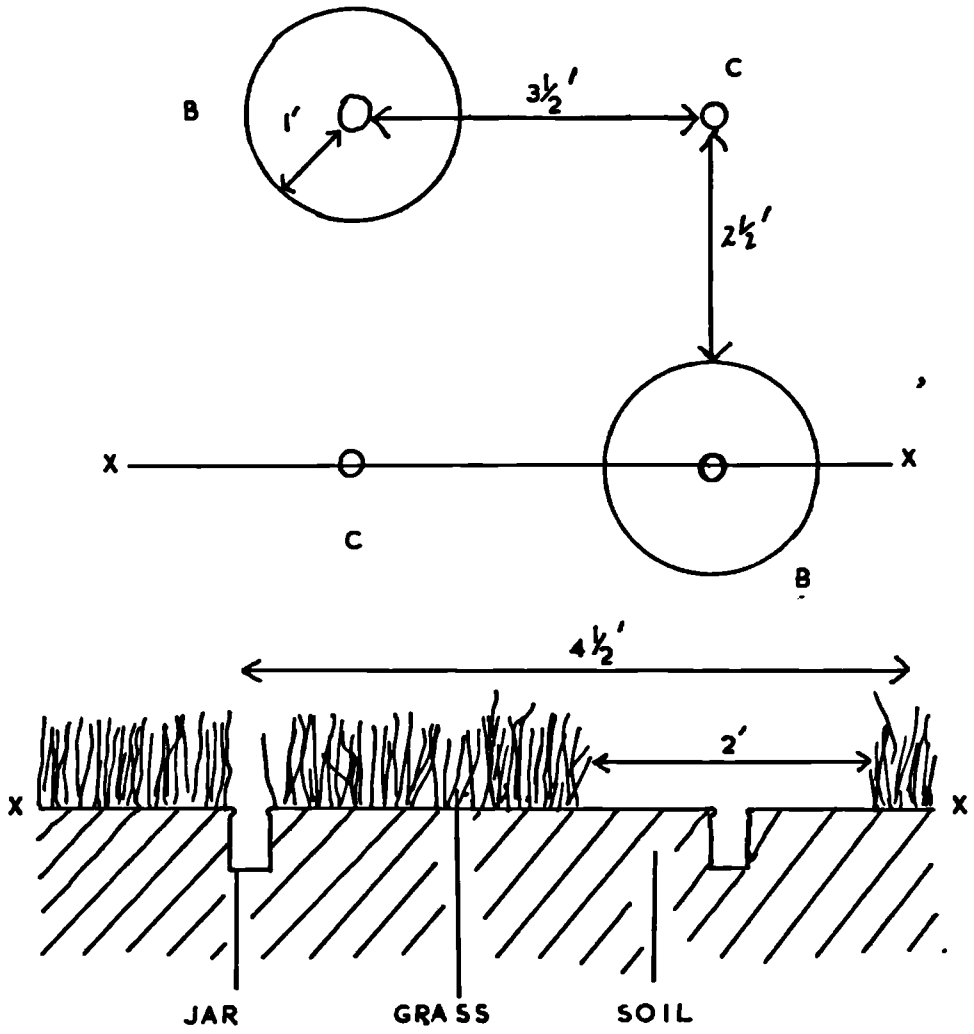


FIG.2. ARRANGEMENT OF TRAPS IN PLOT 2., WHERE B,C, ARE TRAPS.

Trap	1	2	3	4	5
Nebria catch	47	76	90	55	28
Litter depth (ins.)	0.93	030	0·05	0·45	1·25

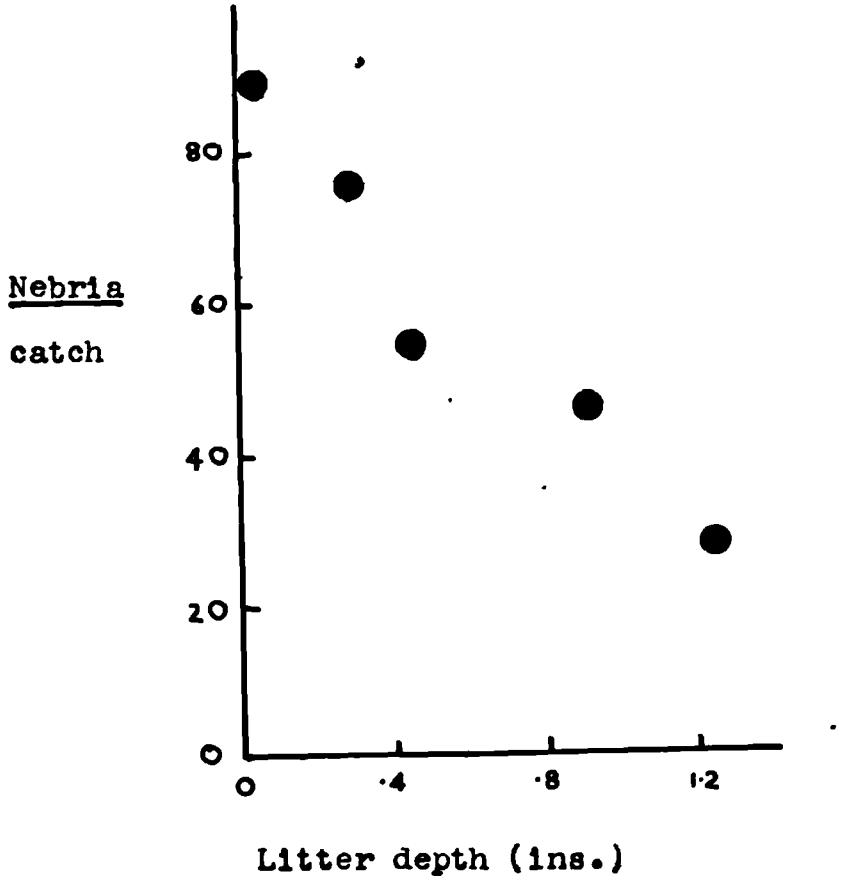


Fig.3 Catch of Nebria and litter depth in South Lodge Wood transect. 1959.

Fig.4

Daily catches of Carabidae in 23 permanent traps : I3/4/59-30/7/59.

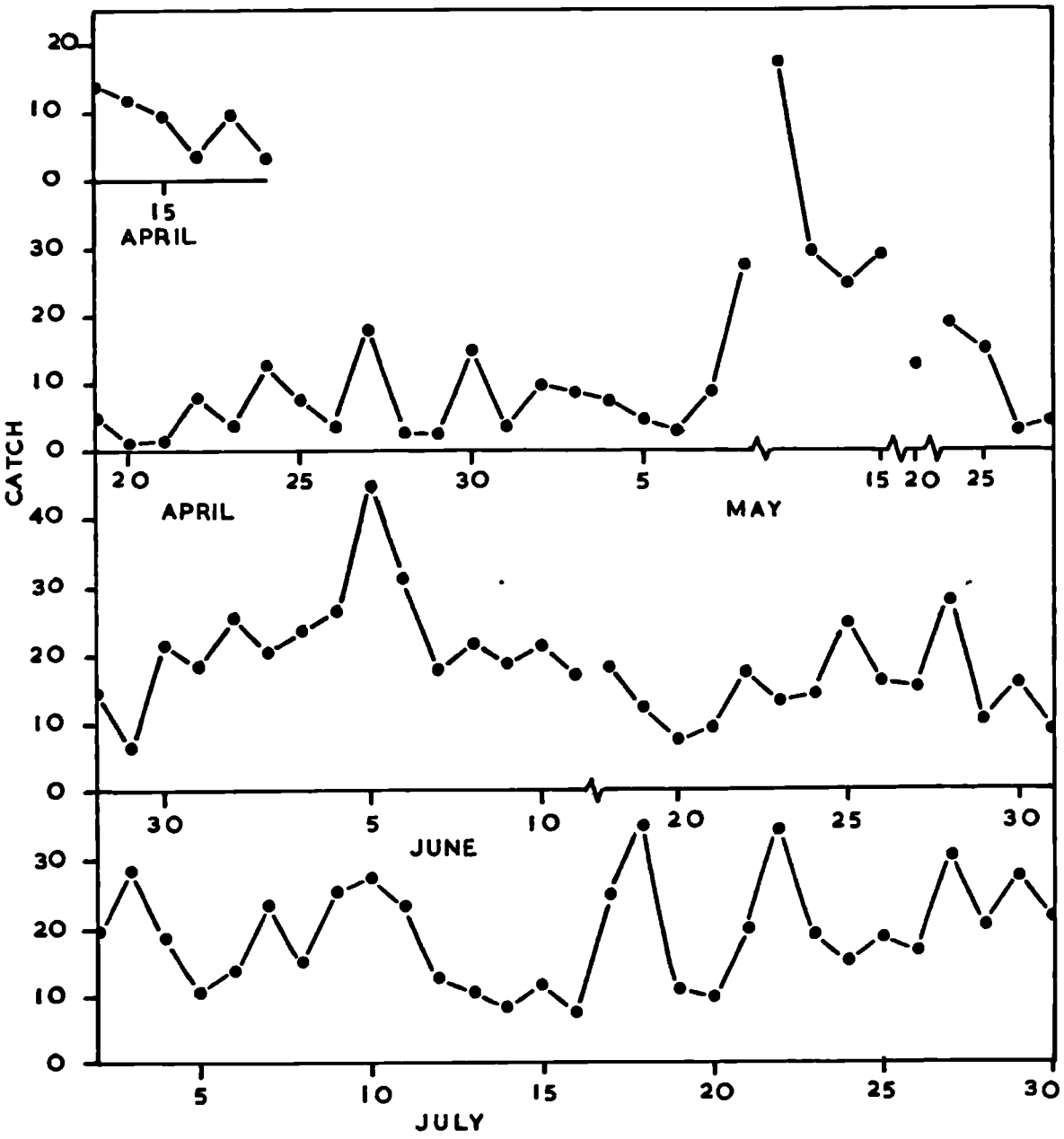


Fig.5

Daily catches of 34 traps, and Grass Minimum temperature 6/6/59-30/7/59 .

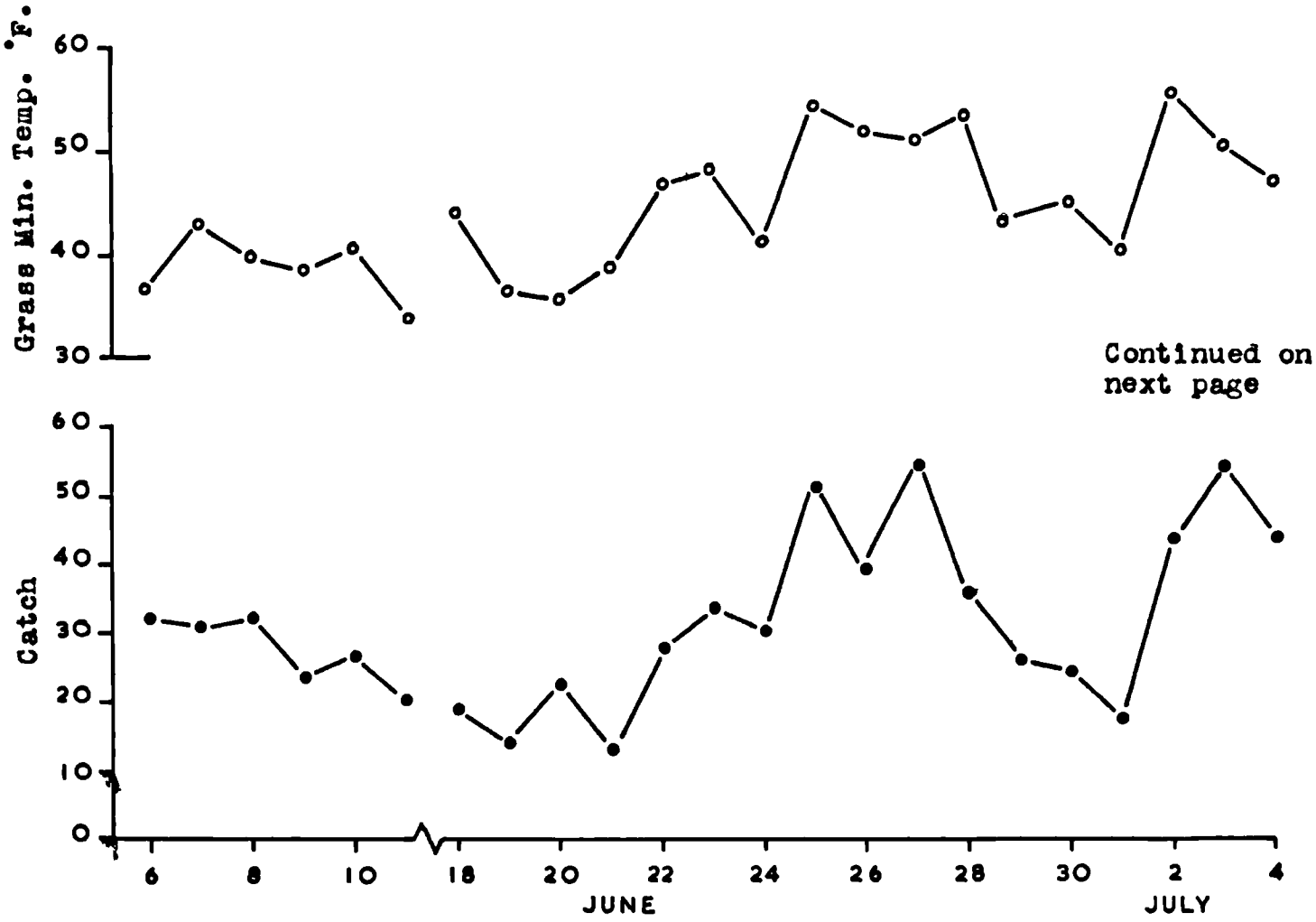


Fig.5
(Continued)

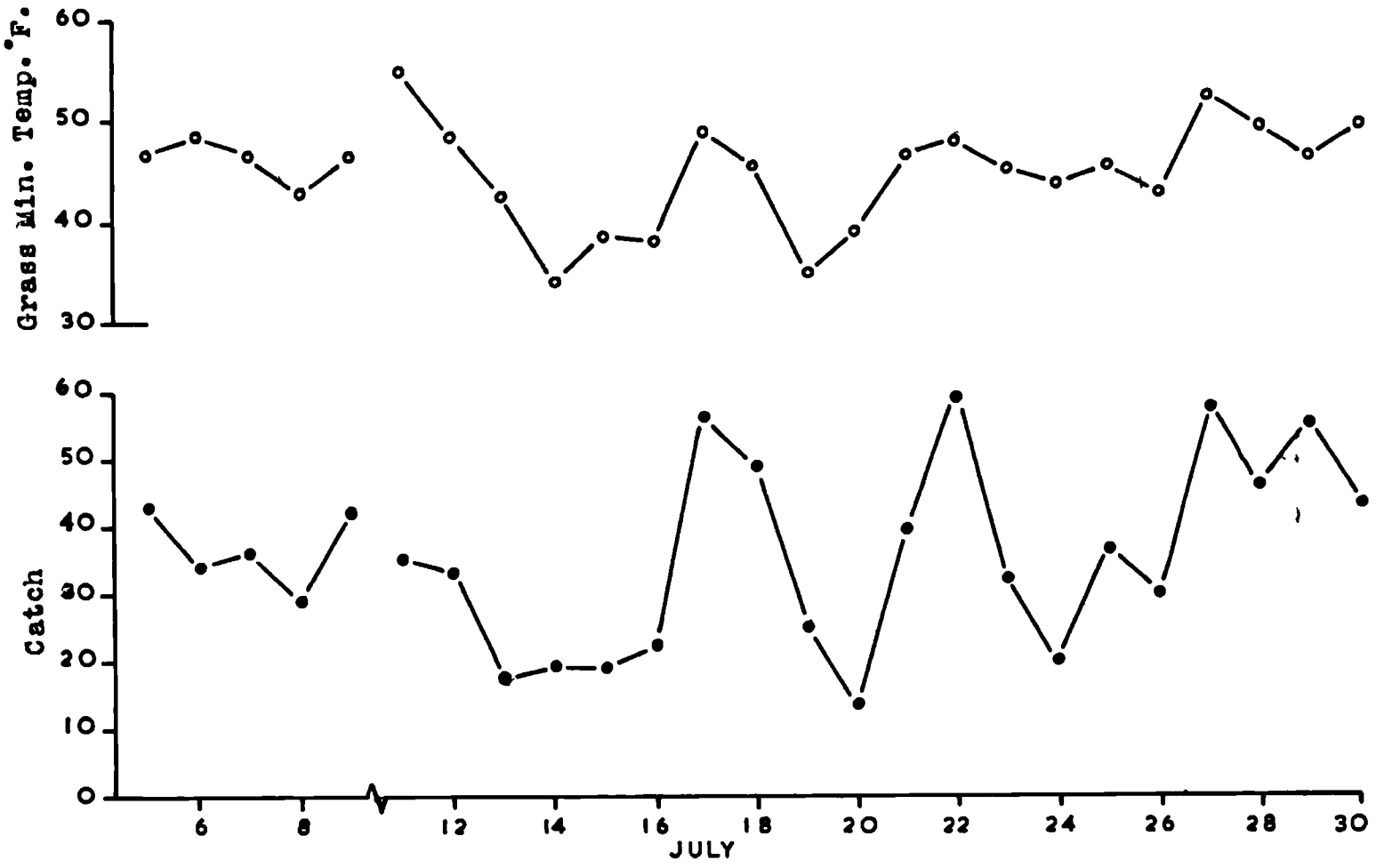


FIG. 6

Plots X,Y,Z, South Lodge Wood, to show the effect of distance between traps on catch ;
I 2 3
where o , o , o , etc., are traps.

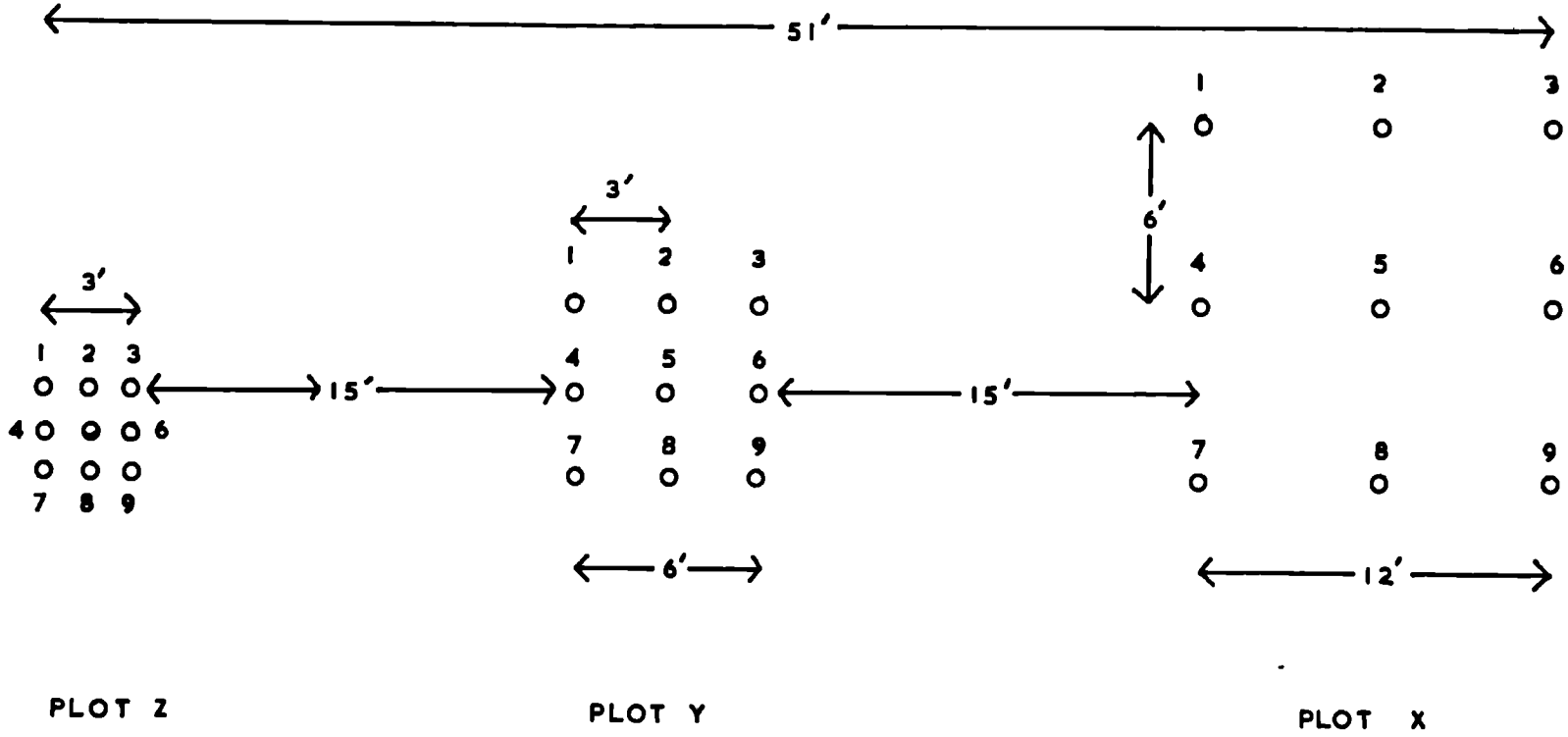
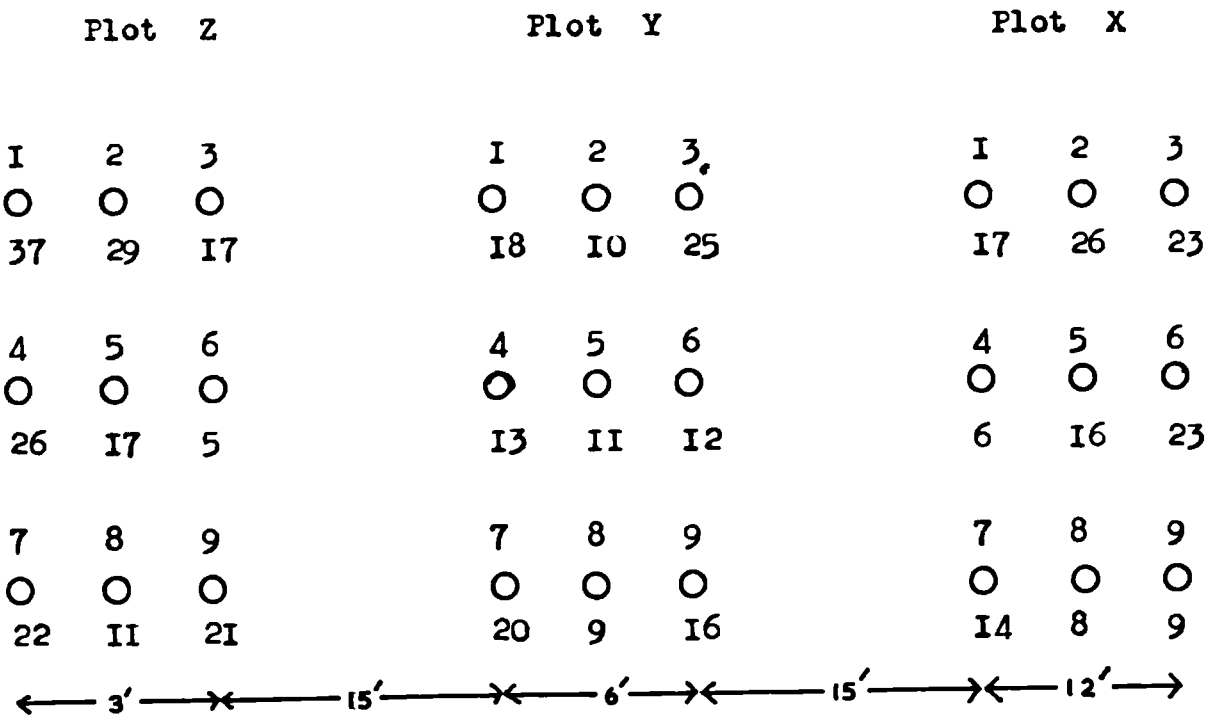


FIG. 7.

Distribution of Nebria brevicollis in Plots X, Y, Z, South Lodge Wood, _ 6/5/59-6/6/59.

I 2 3
O, O, O, ... represent traps, and the lower row of figures, catch.



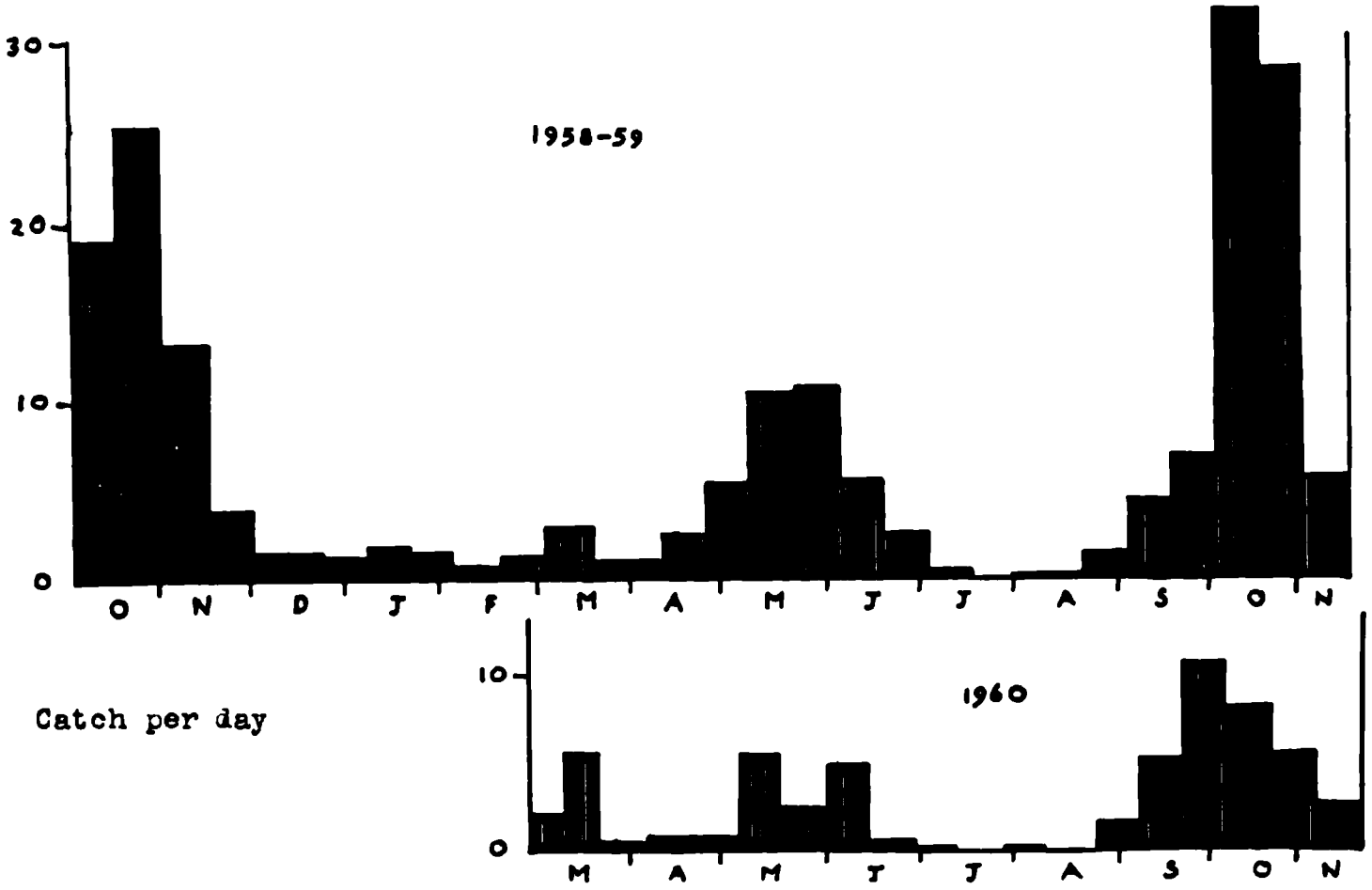


Fig.8. Annual catches of N.brevicollis adults.23 Traps 1958- 9.

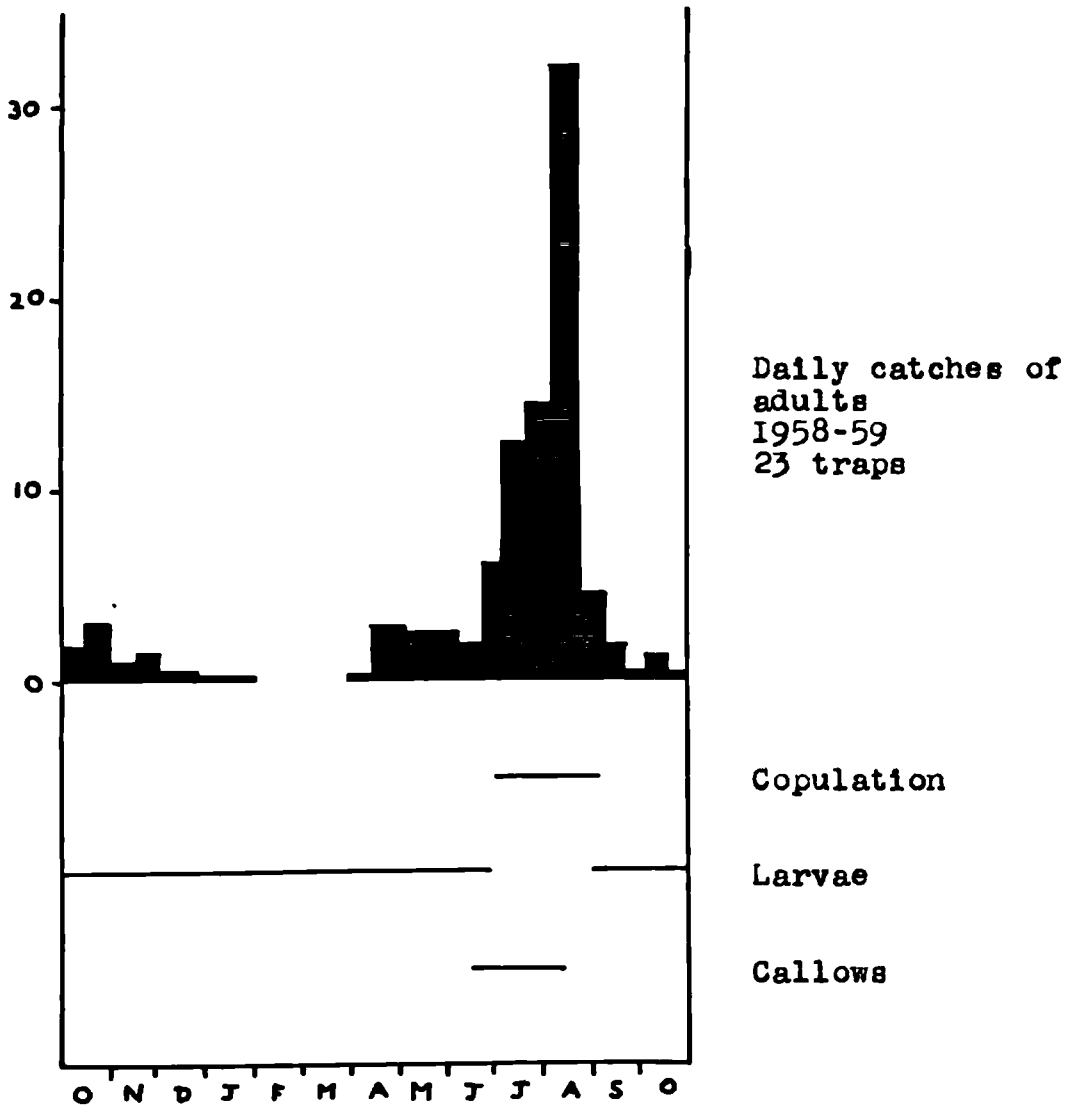


Fig.9. Life history of Pterostichus madidus

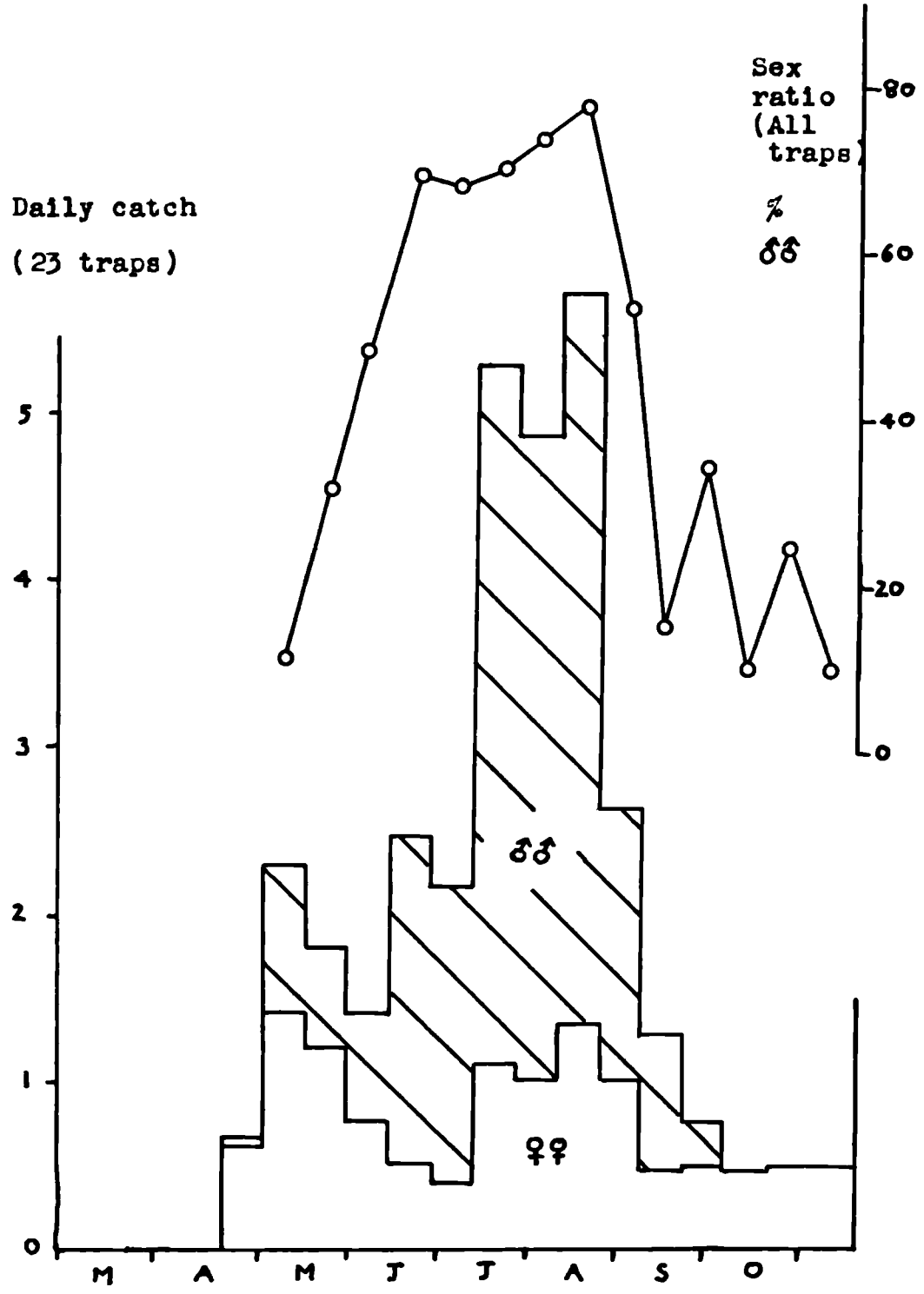


Fig.IO. P.madidus. Catches and changes in the sex ratio. I960.

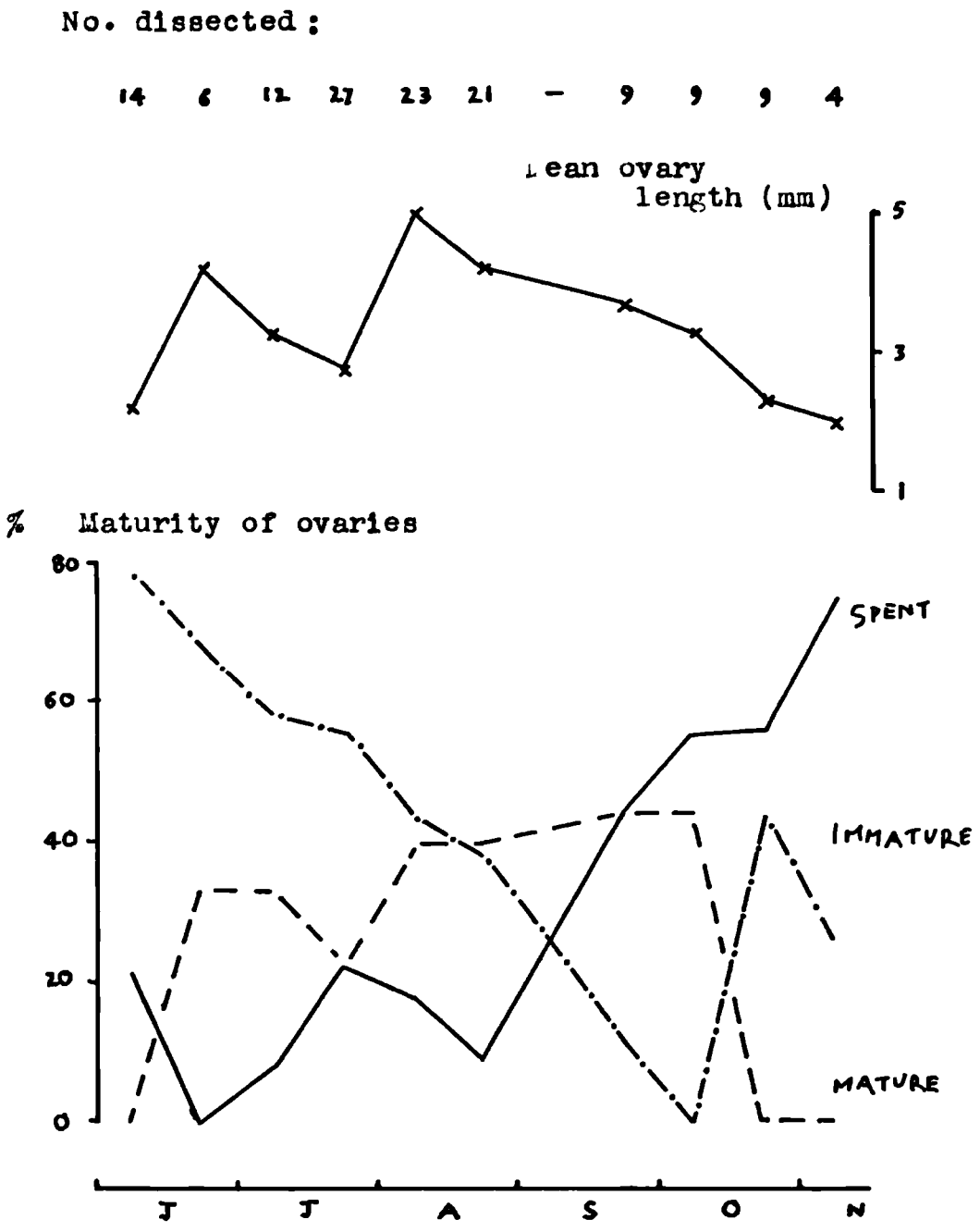


Fig.II. P.madidus. Condition of ovaries. 1960.

Fig.I2. Annual catches of adult Carabidae 25 spp.

I	23 traps	I958-59	
2		I960	
3	Transect 2	I959	Scale
4		I960	
5	Hill Bottom	I959	(catch/day)
6		I960	x 10
7	Wood Bank	I960	
8	Elm Hill heath	I960	

20
10
0

Vertical lines show the limits of trapping periods

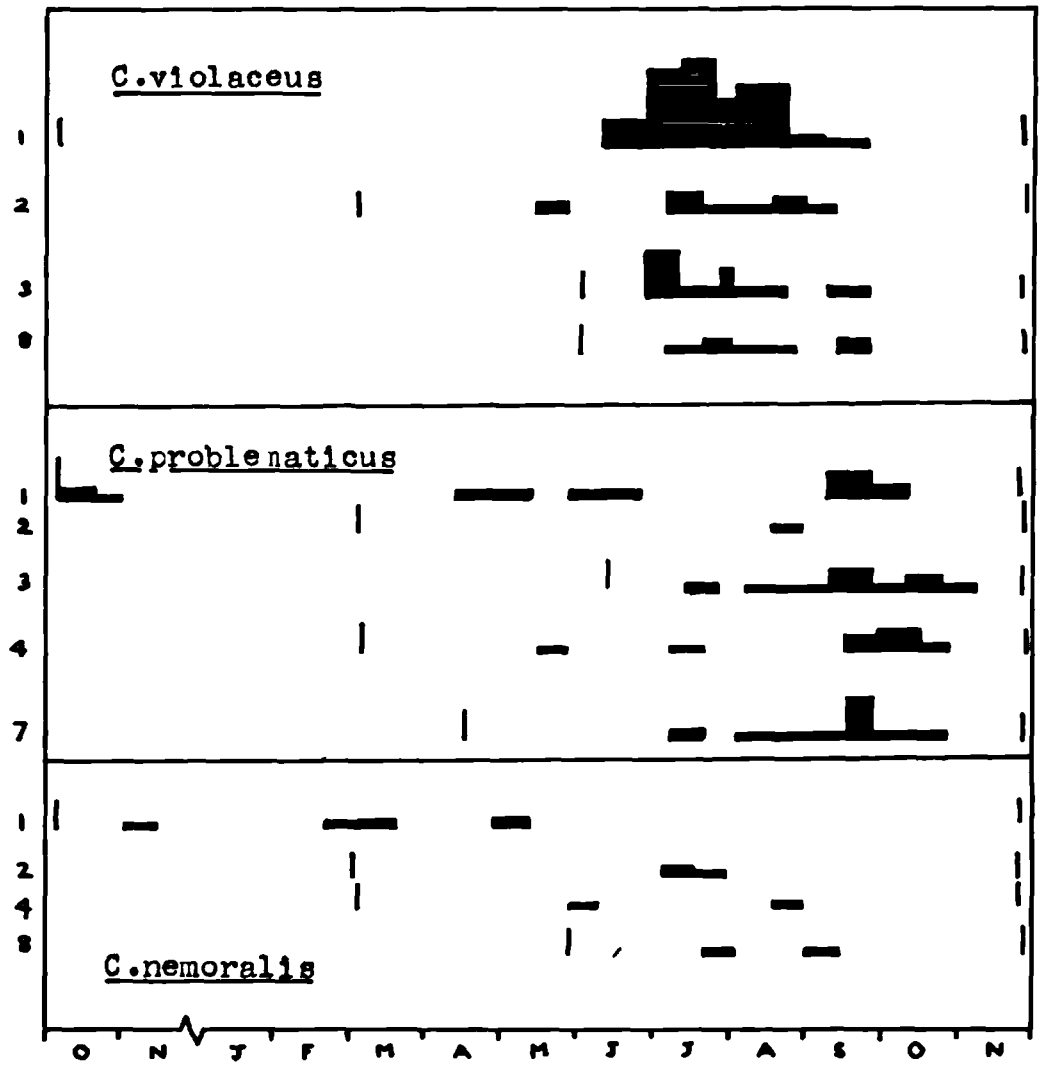


Fig.I2. (Continued)

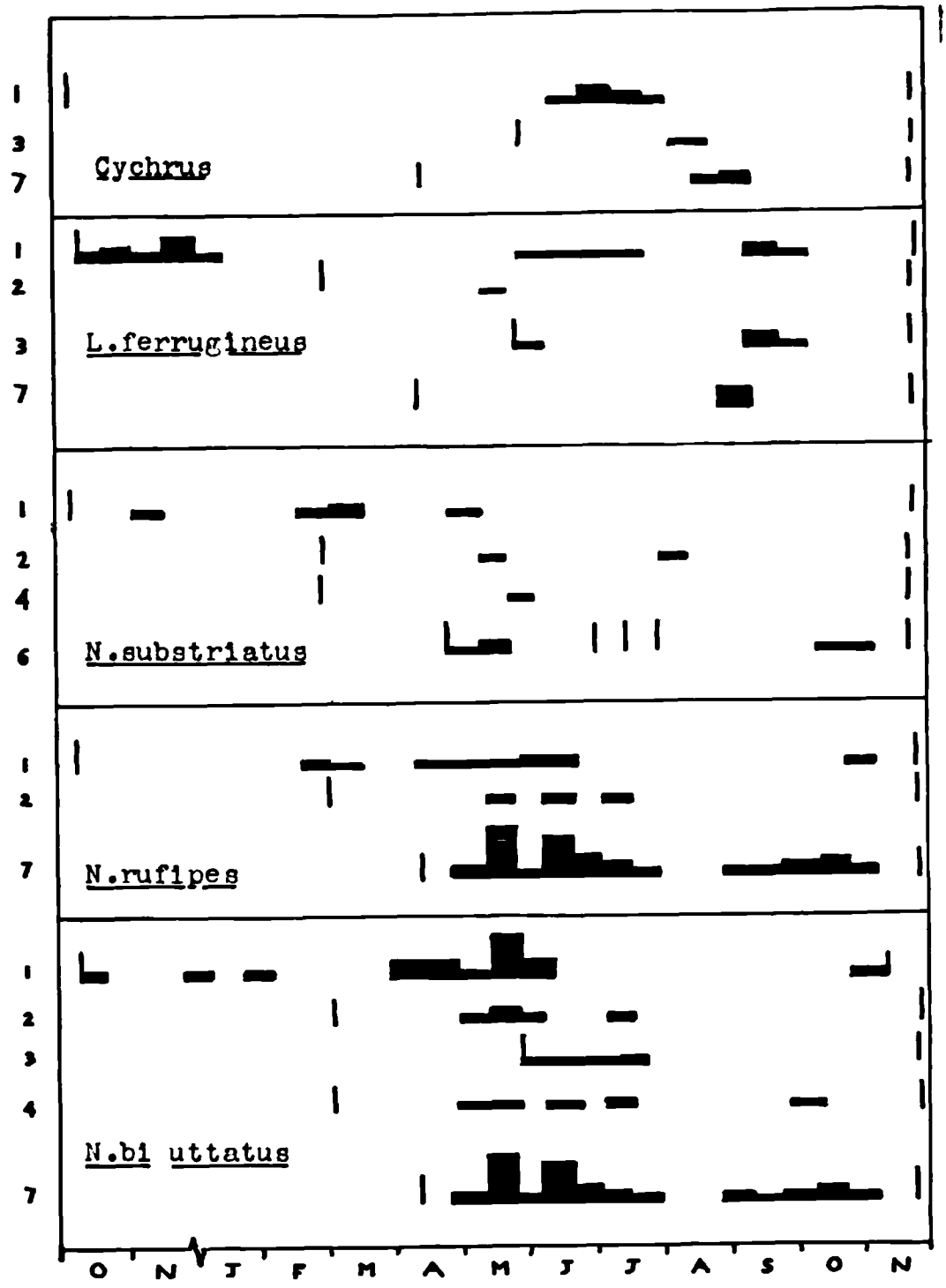


Fig.12. (Continued)

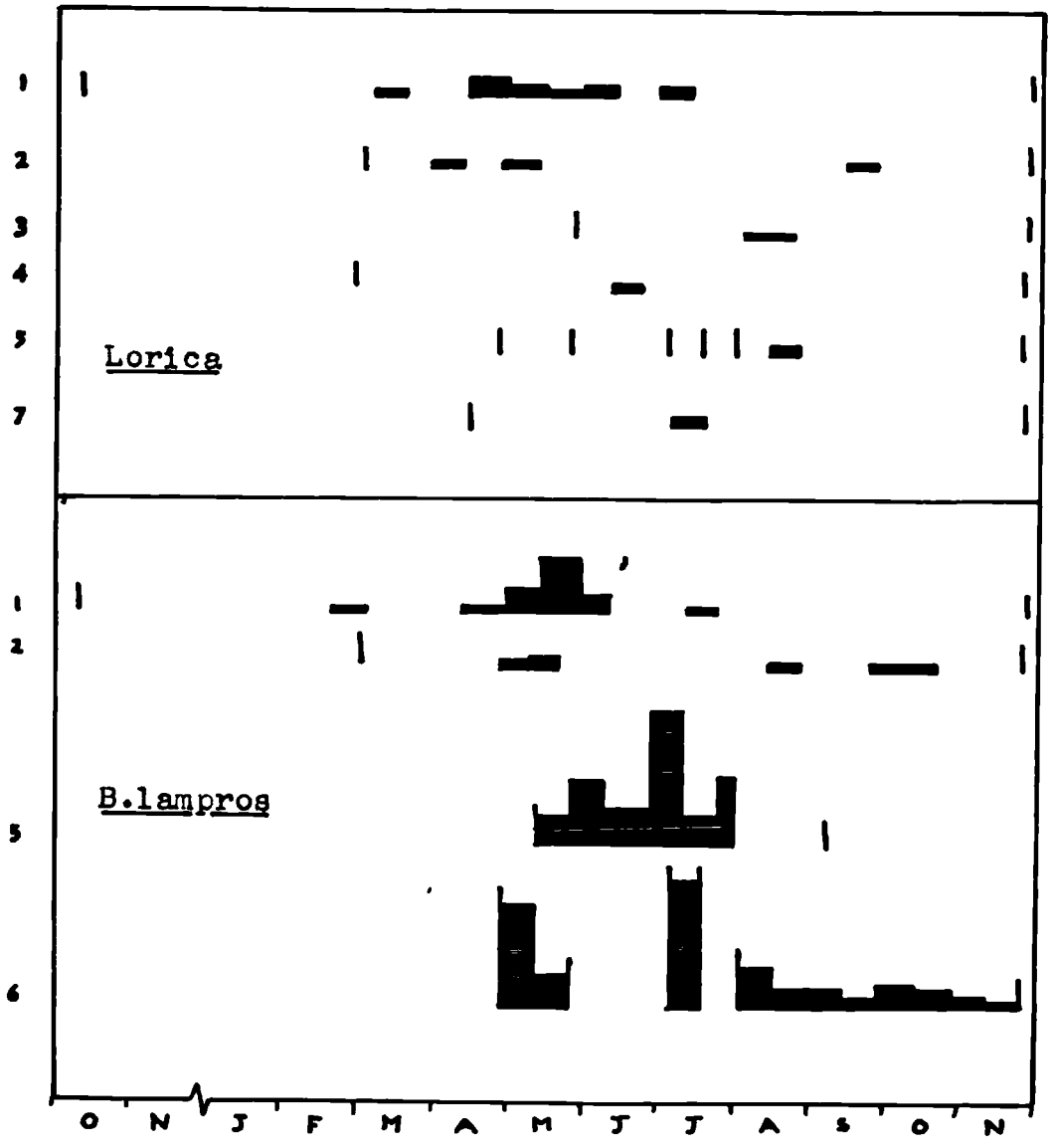


Fig.12. (Continued)

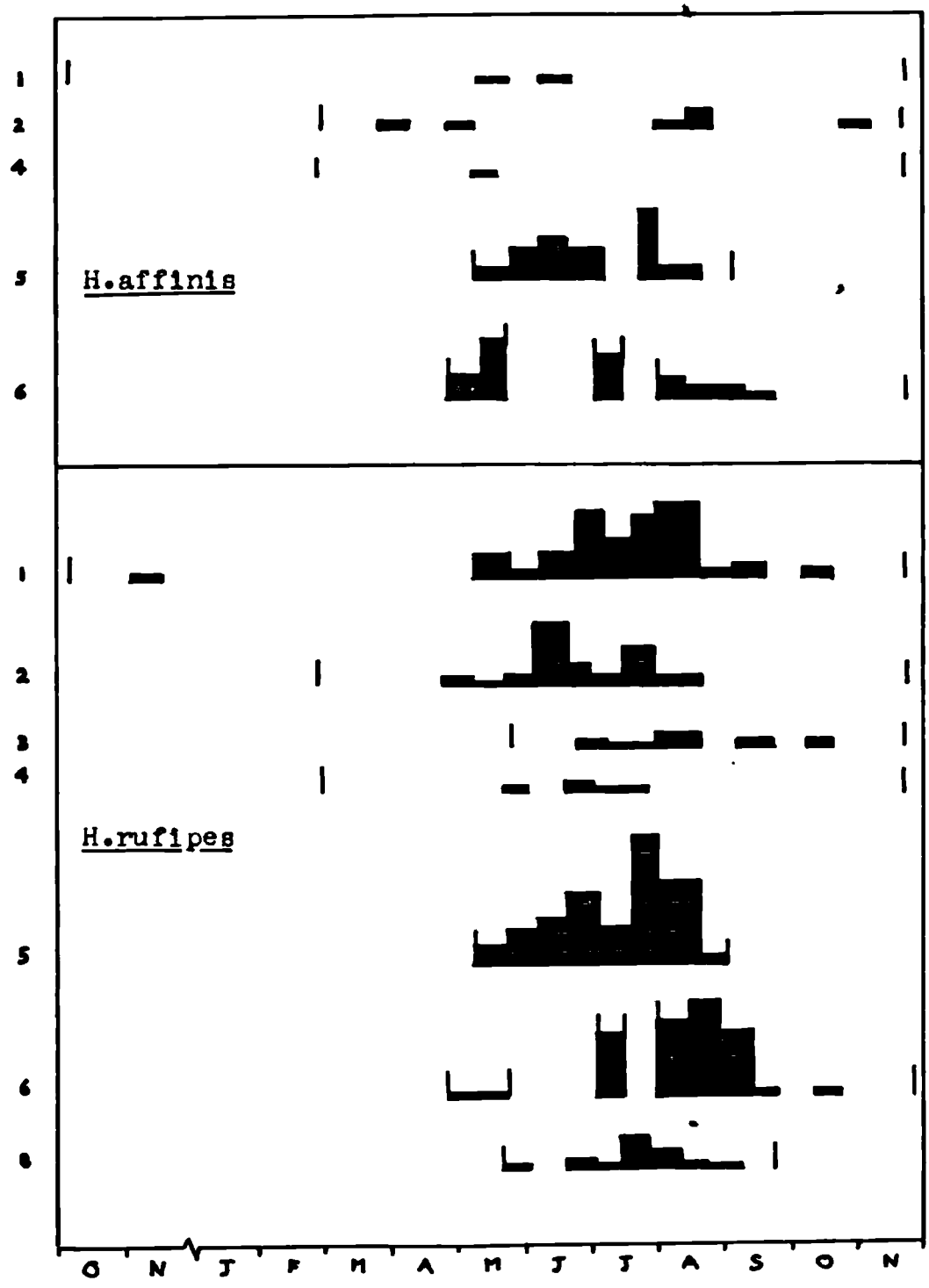


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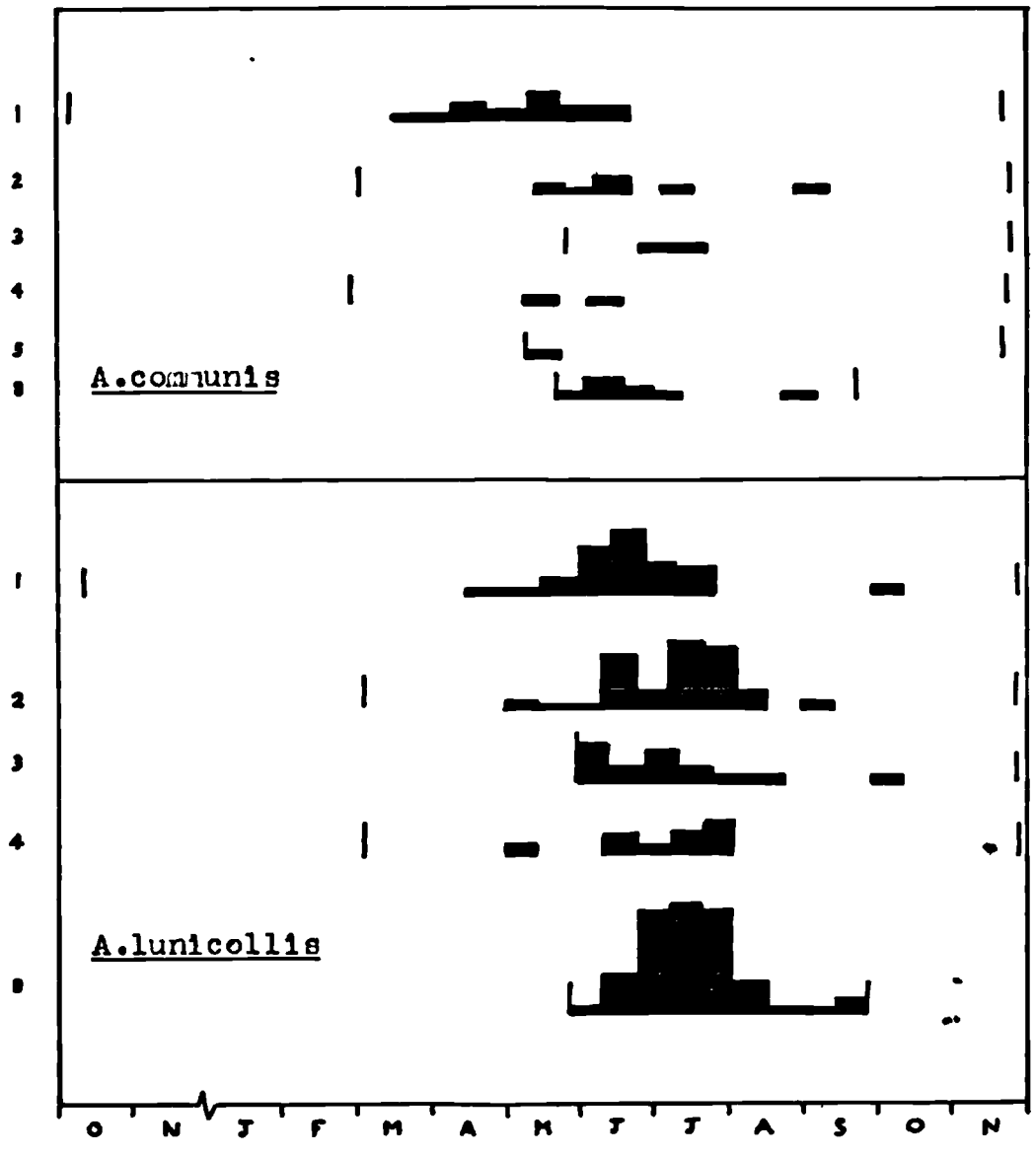


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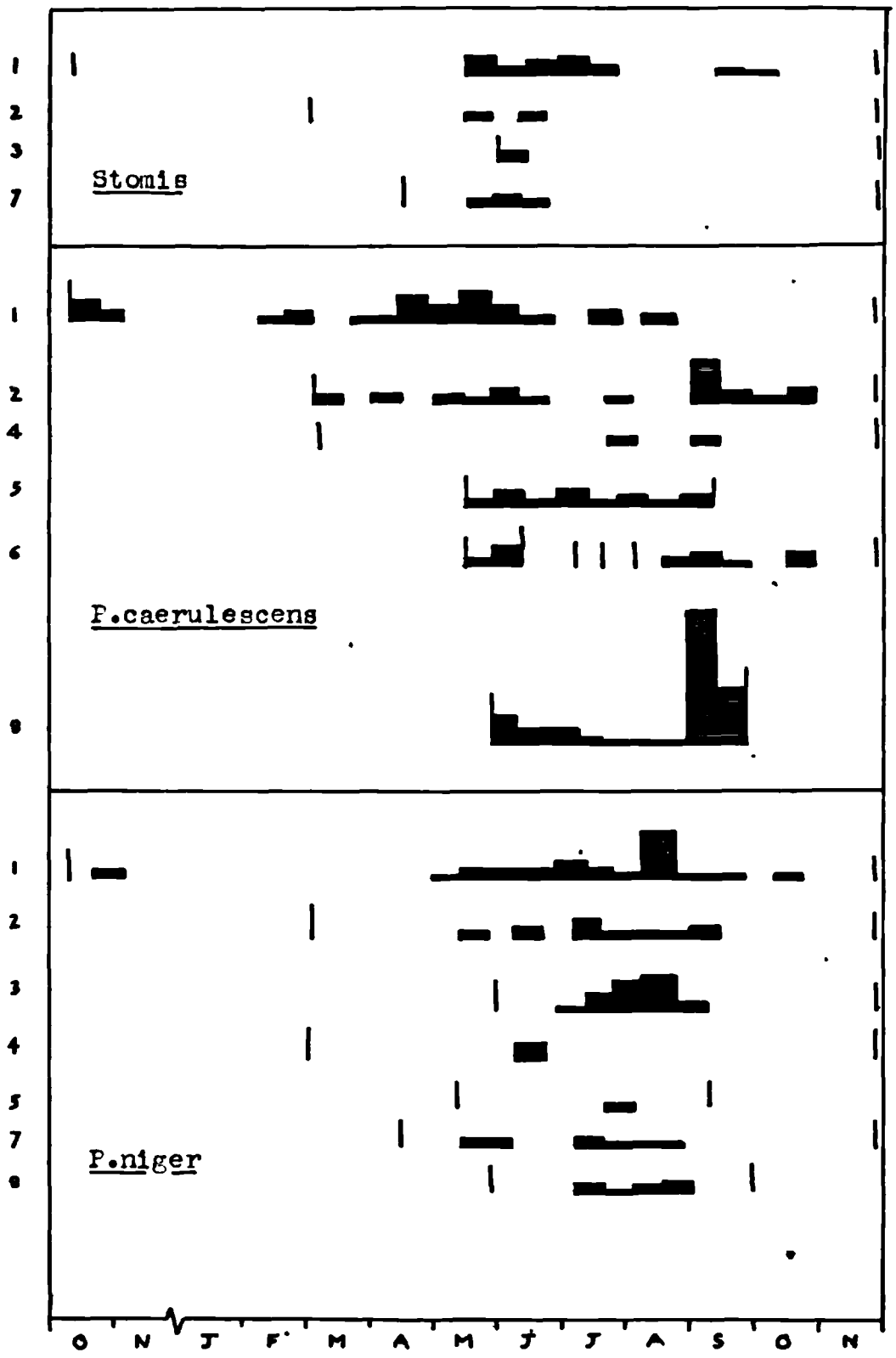
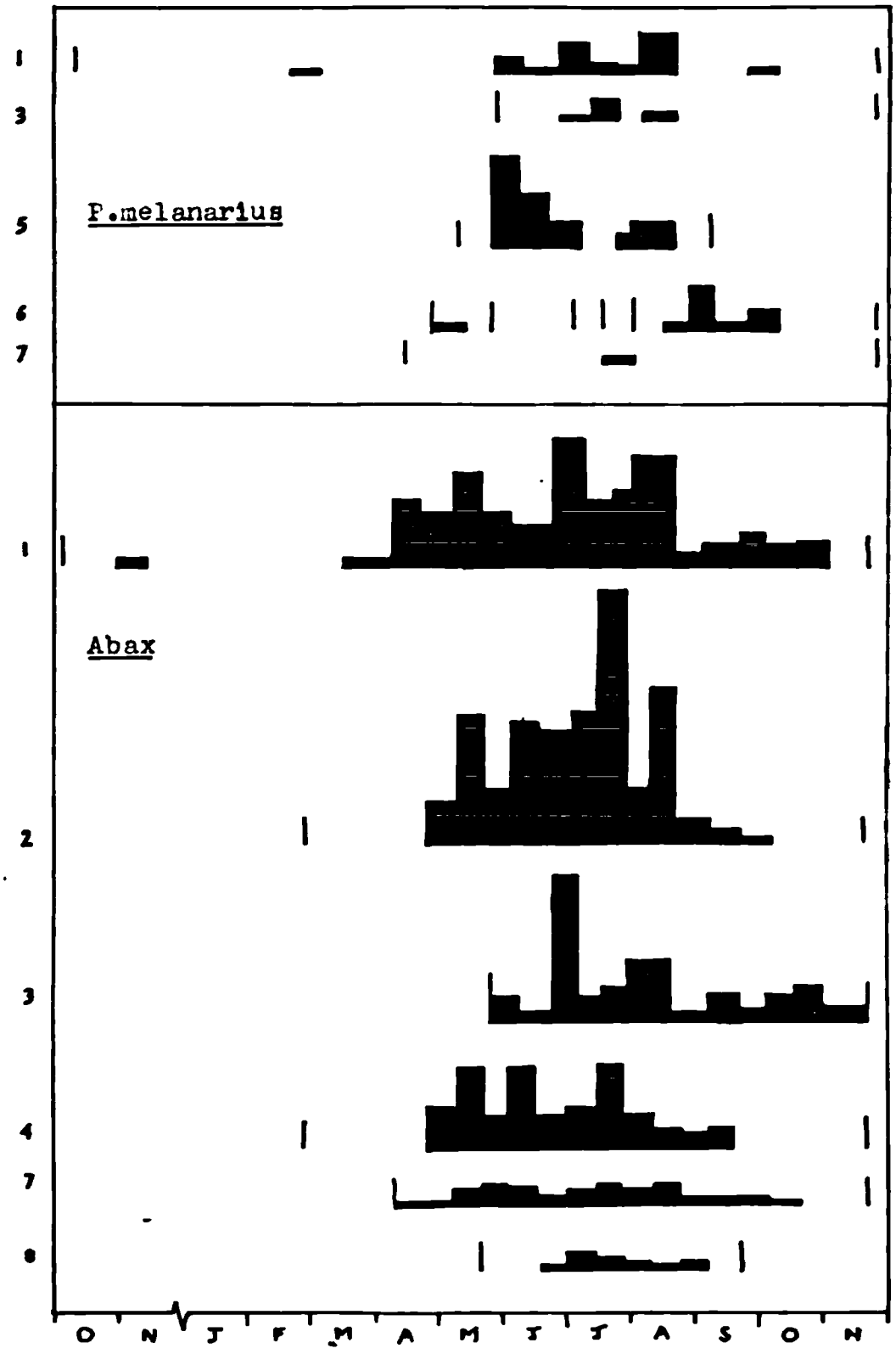


Fig.I2. (Continued)



Fig,12. (Continued)

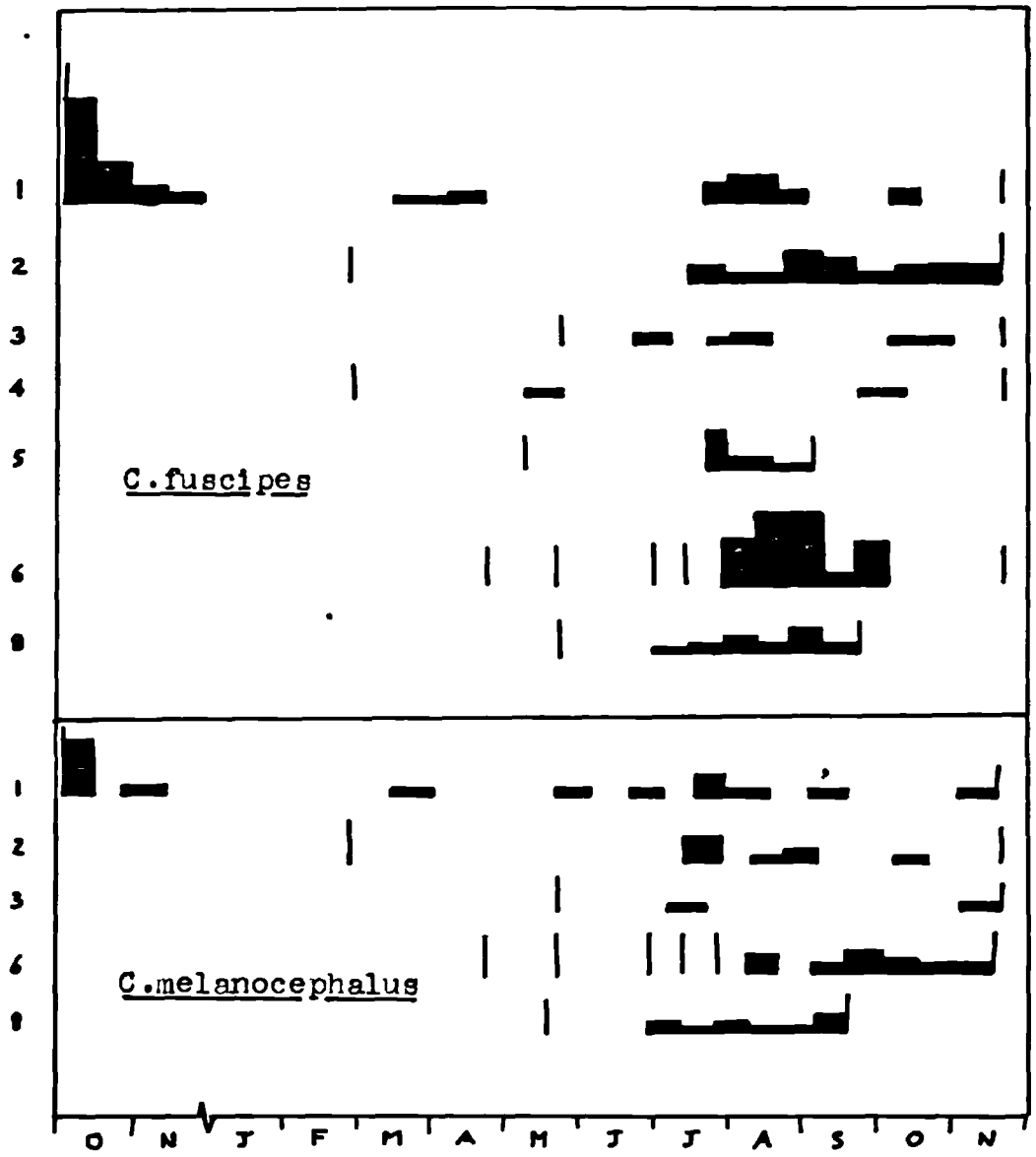


Fig.12. (Continued)

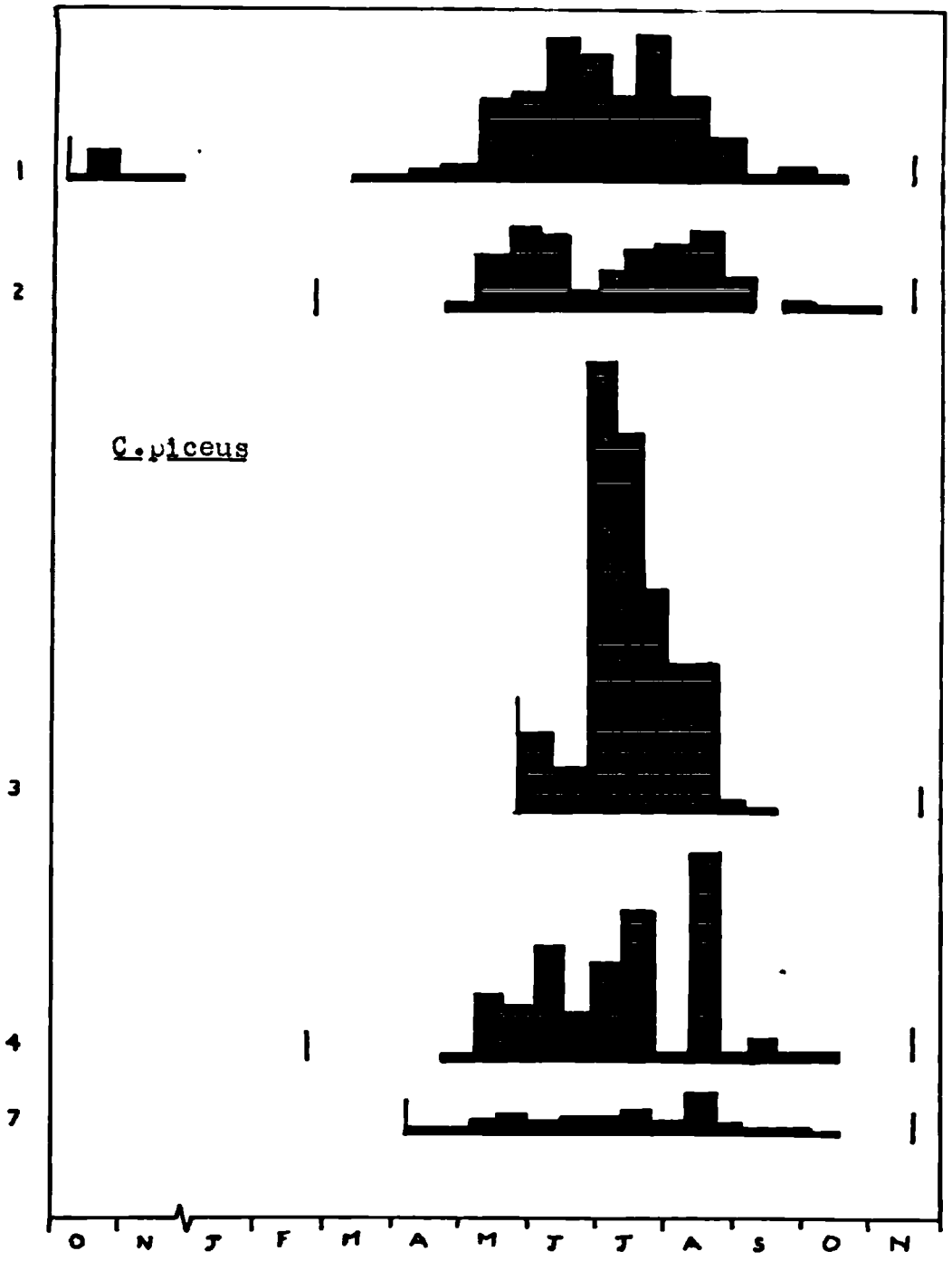
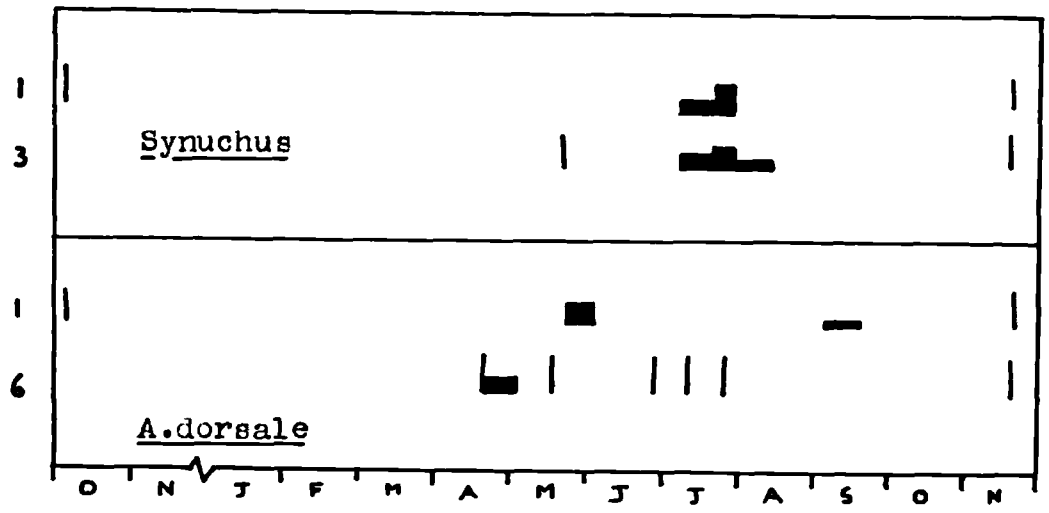
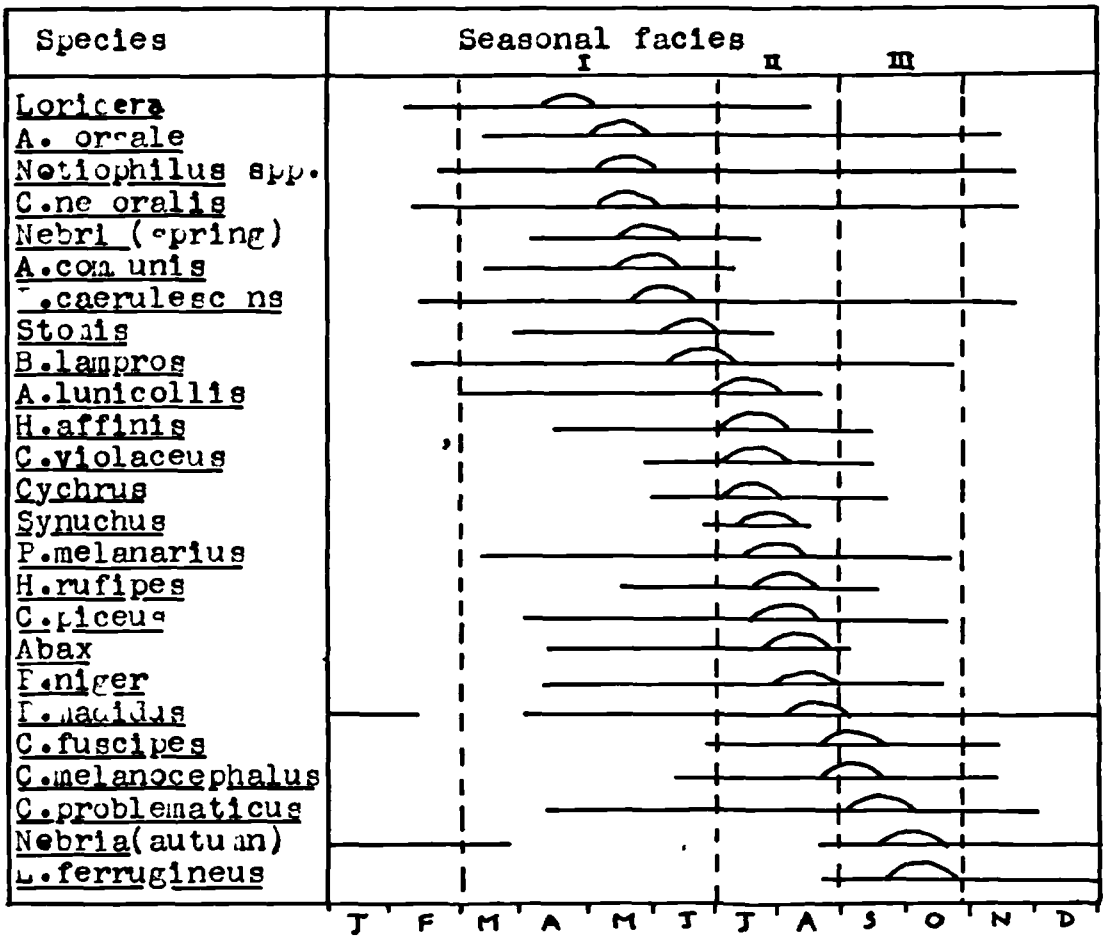


Fig.12. (Continued)



Fi .I2a. Summary of annual activit in Carabid species. 1958-60.

——— More than occasional individuals trapped
⌓ Month of maximum frequency



Seral relationships between vegetation types on the Imperial College Field Station.

Fig.13. (Stages involving podsols do not occur at Silwood)
Modified after Tansley (1953)

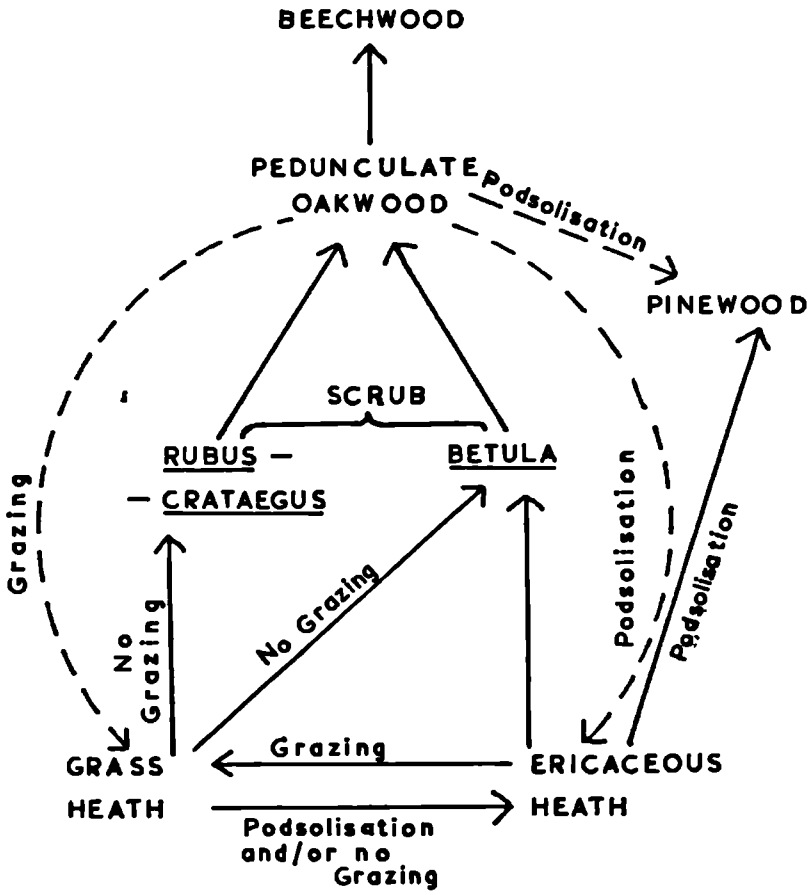


Fig.14.
Distribution of Carabidae in Transect I, Elm Hill.

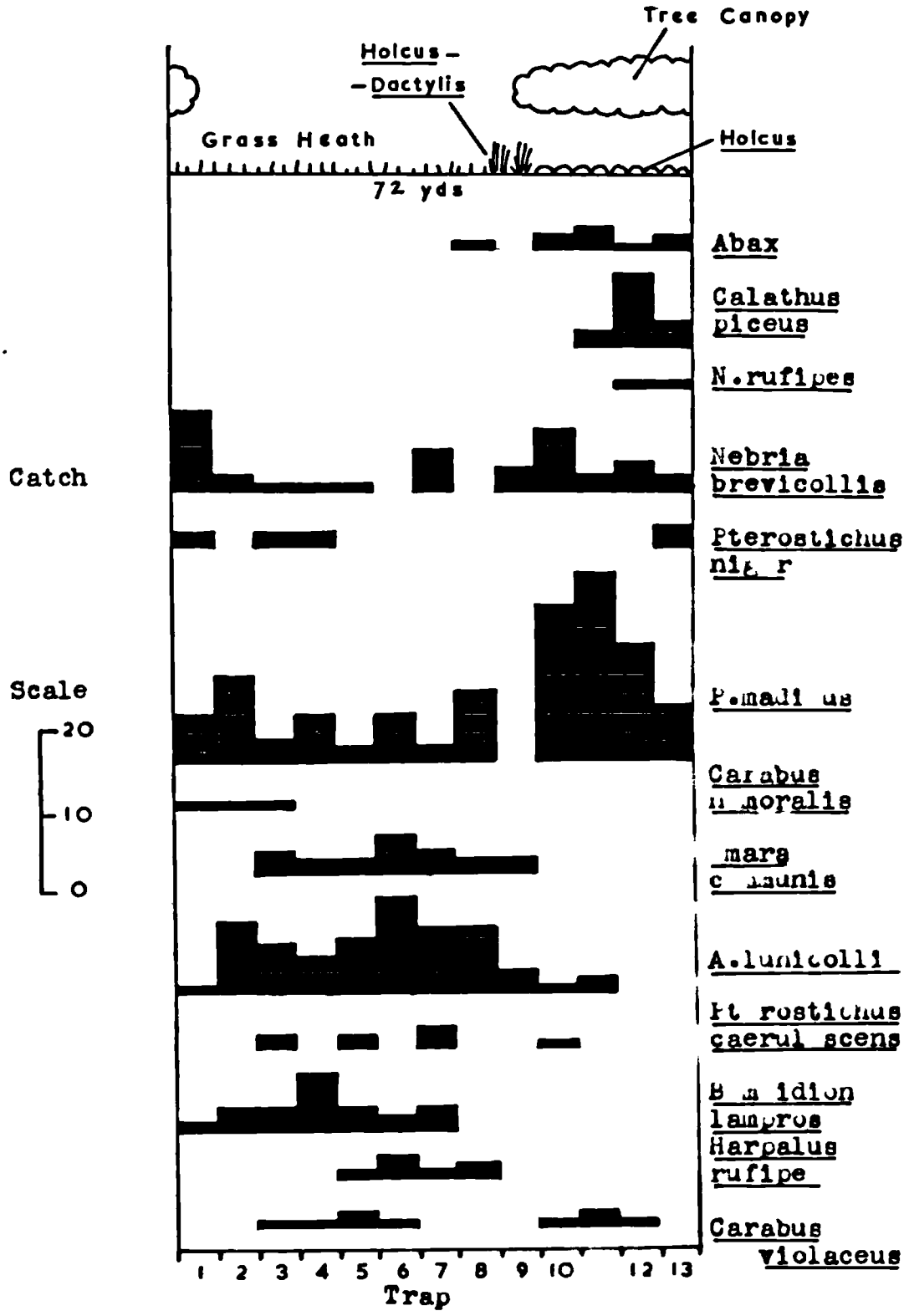


Fig.15. Distribution of Carabidae in Transect 2. Elm Hill. 1959 60.

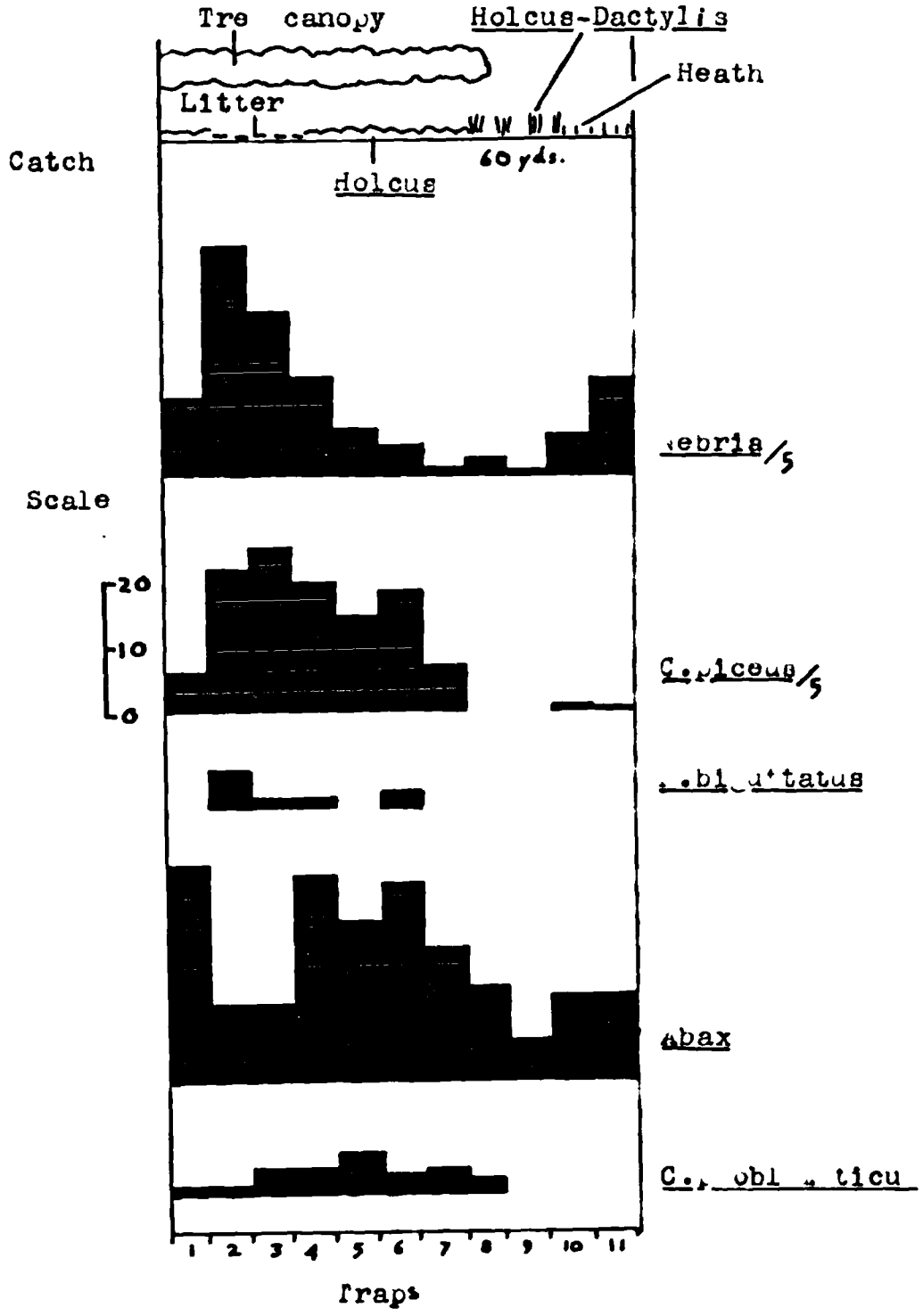


Fig.I5. (Continued)

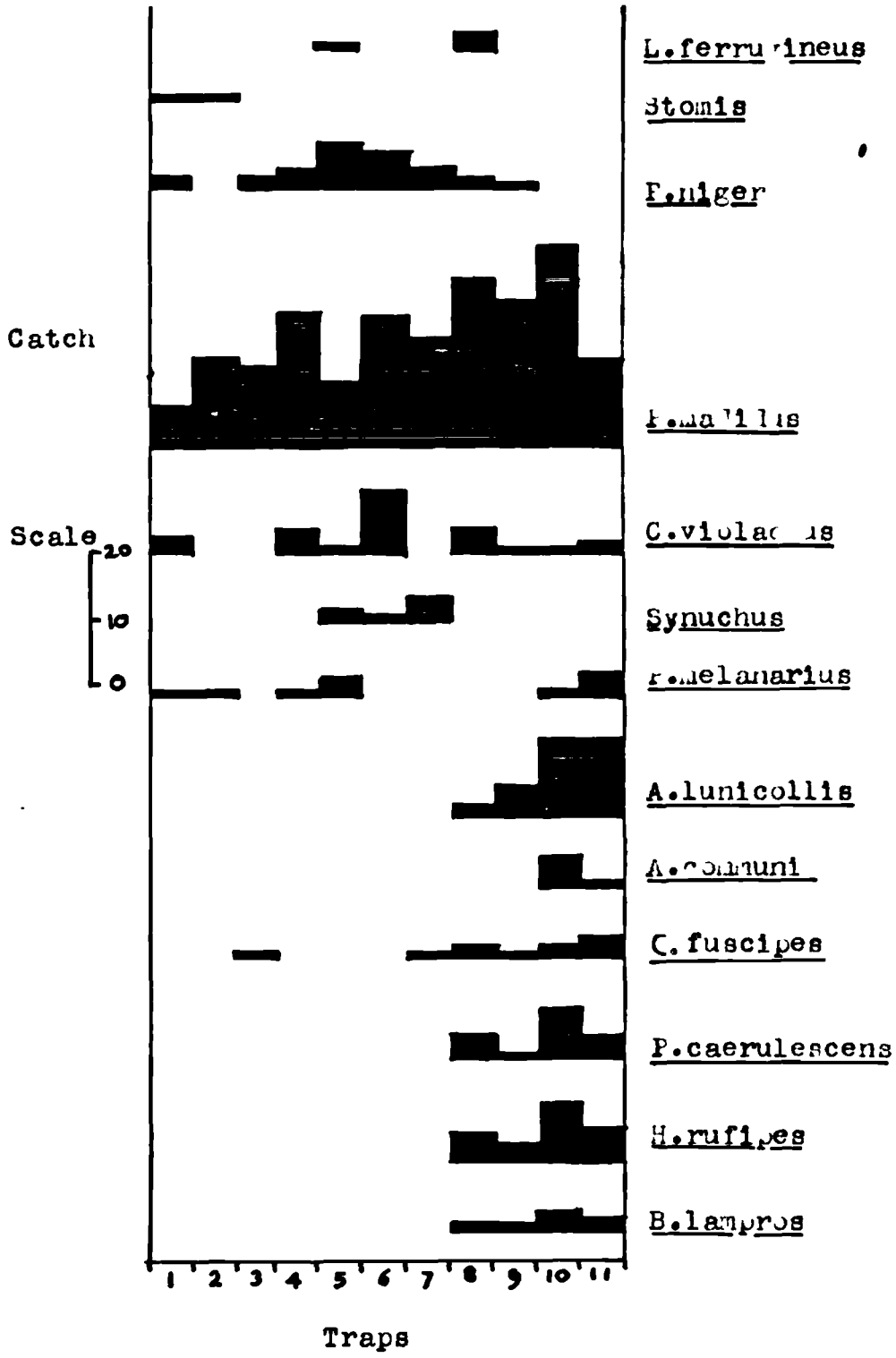


Fig.16. Daily variation in temperature in three habitats.
(One inch below soil surface)

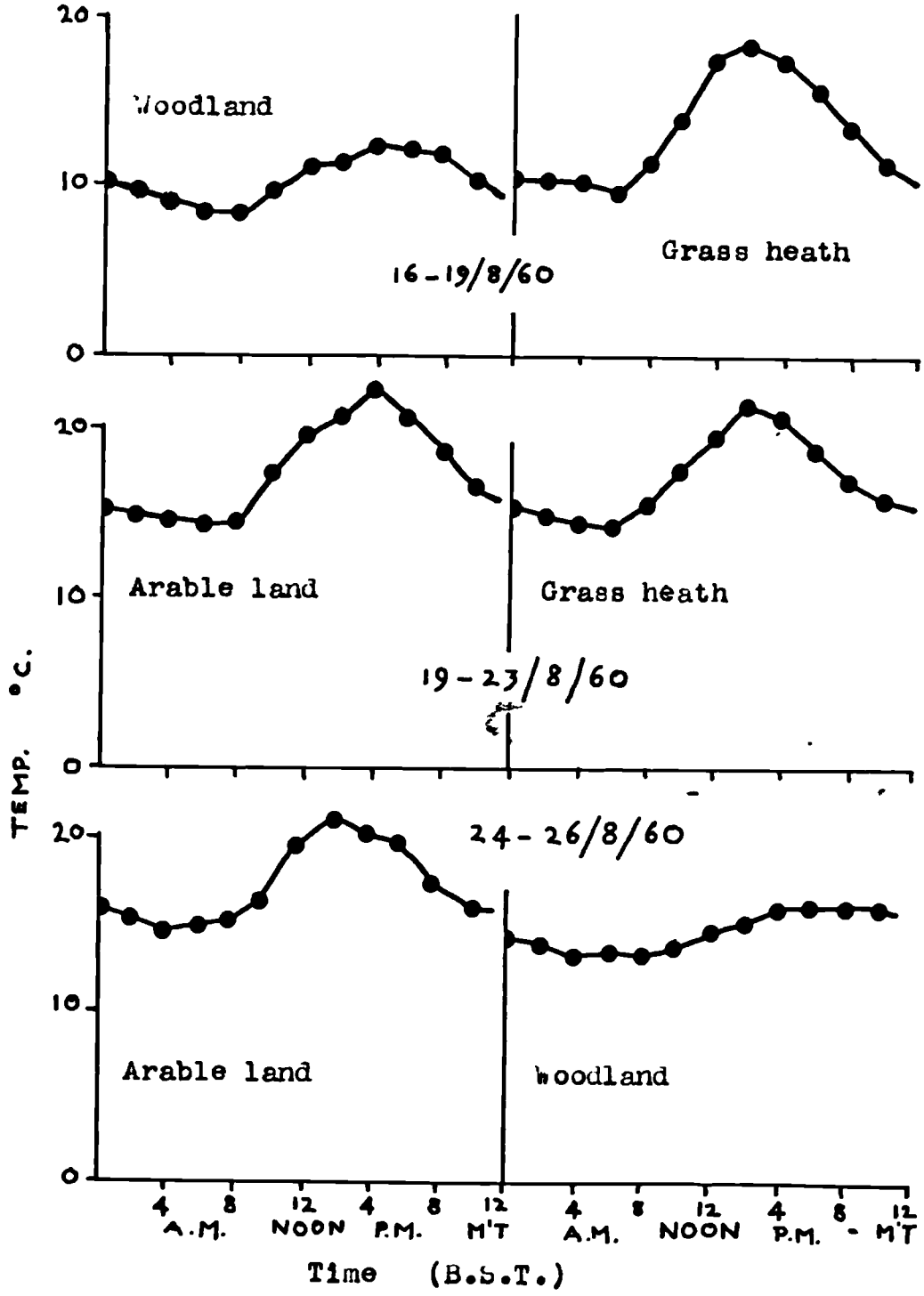


Fig.17.

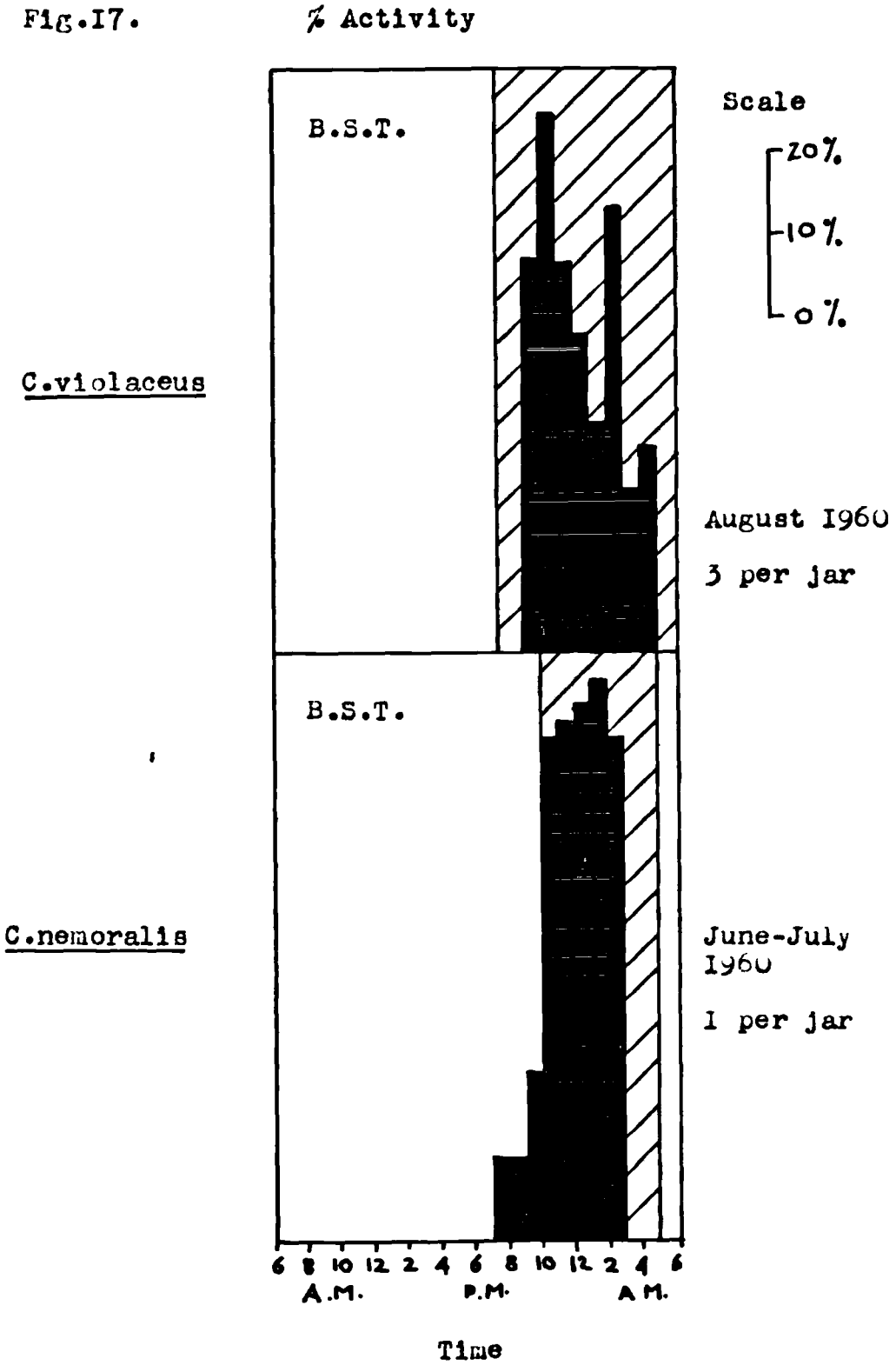

% Activity
B.S.T.
Scale
20%
10%
0%
C.violaceus
August 1960
3 per jar
B.S.T.
C.nemoralis
June-July 1960
1 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.I8.

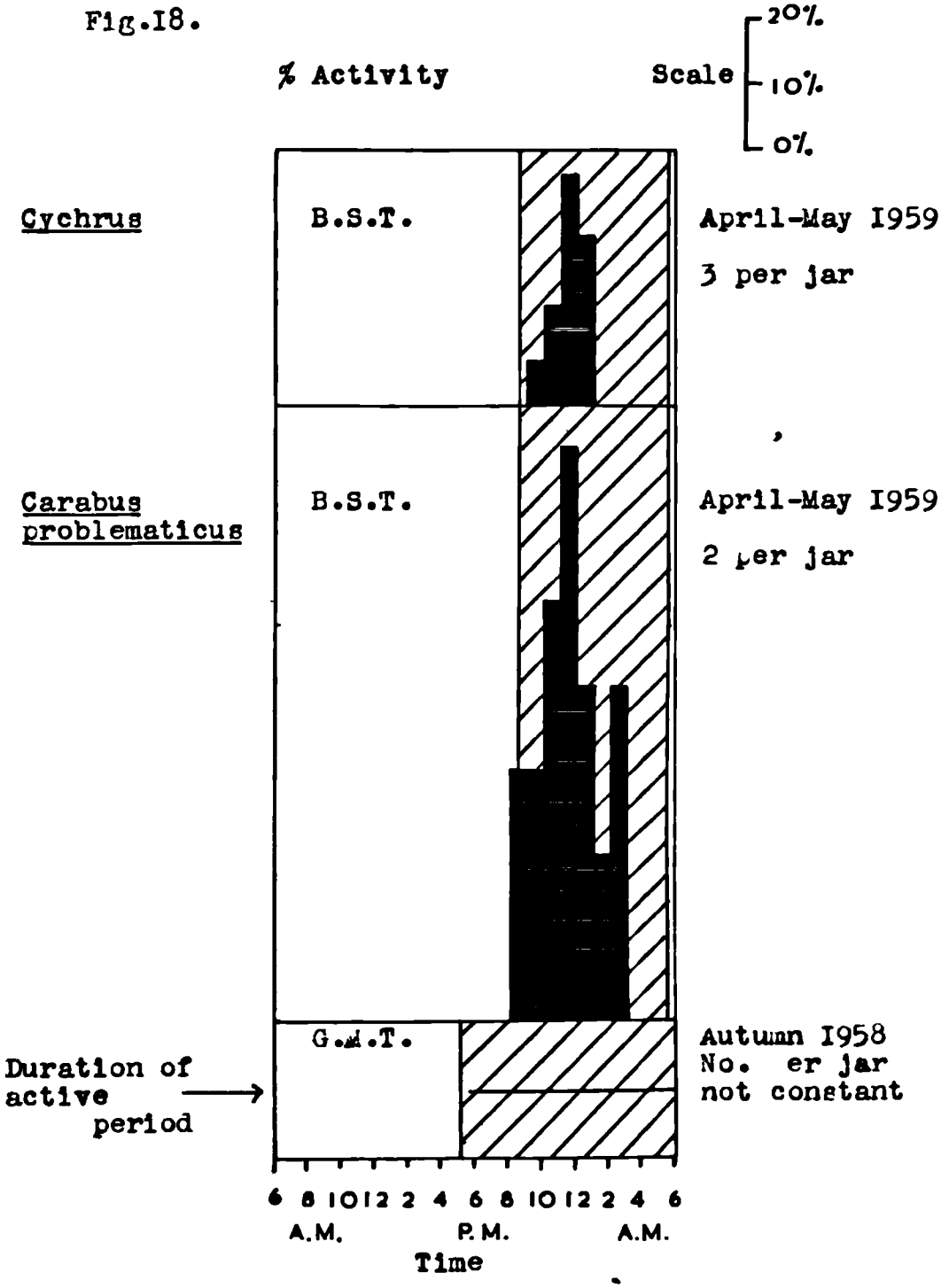
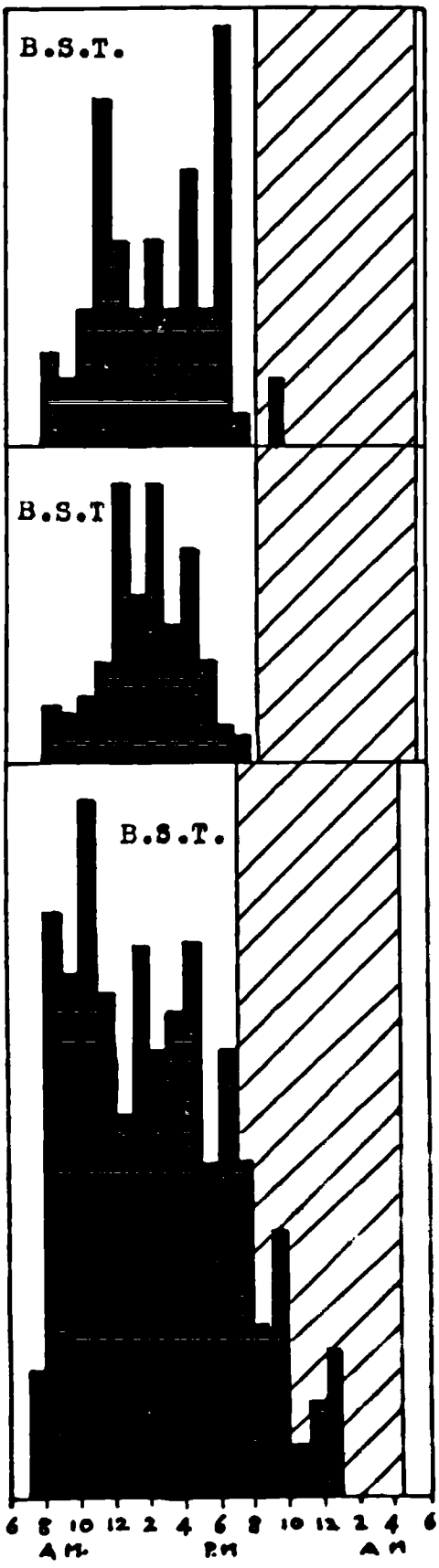

% Activity
Scale
20%.
10%.
0%.
Cychrus
B.S.T.
April-May I959
3 per jar
Carabus problematicus
B.S.T.
April-May I959
2 per jar
G.M.T.
Autumn I958
No. per jar not constant
Duration of active period
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.19.



N.biguttatus — Spring 1959 5 per jar

N.substriatus — Spring 1959 5 per jar

N.rufipes — June-July 1960 5 per j

Time

Fig.20. % Activity Scale 20% 10% 0%

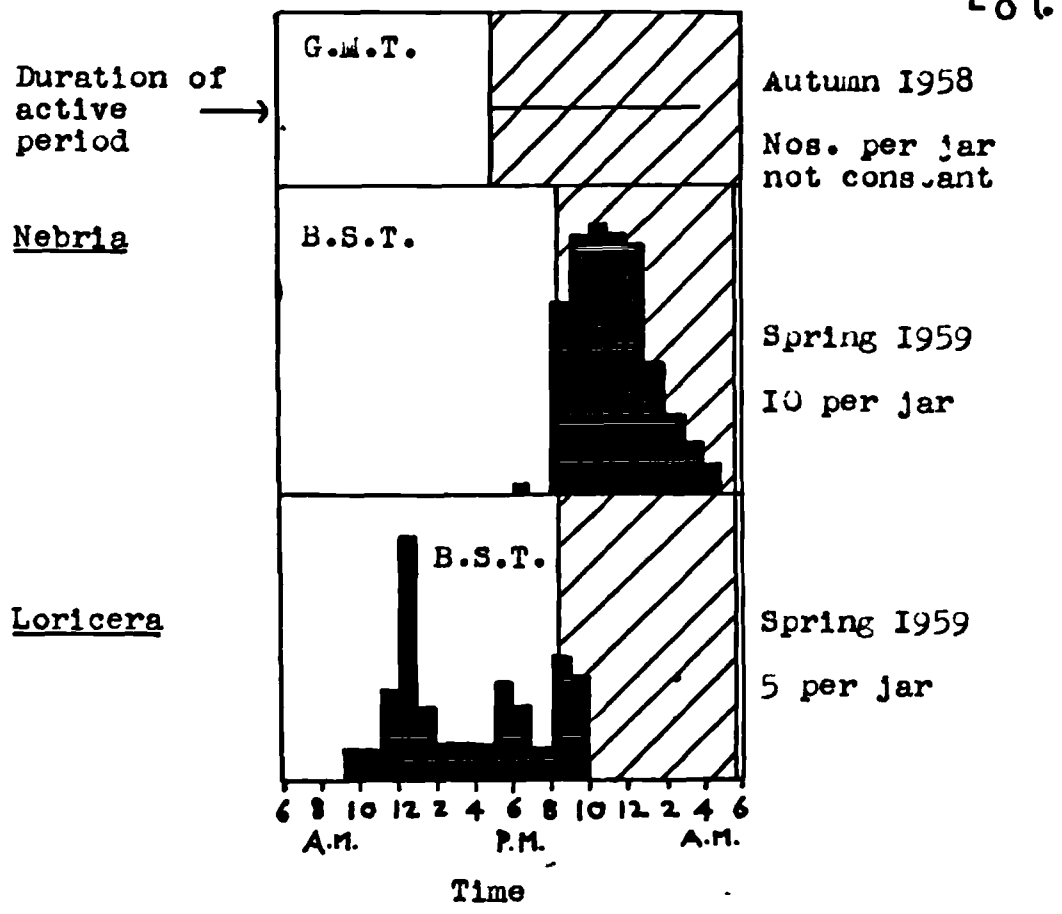


Fig.2I.

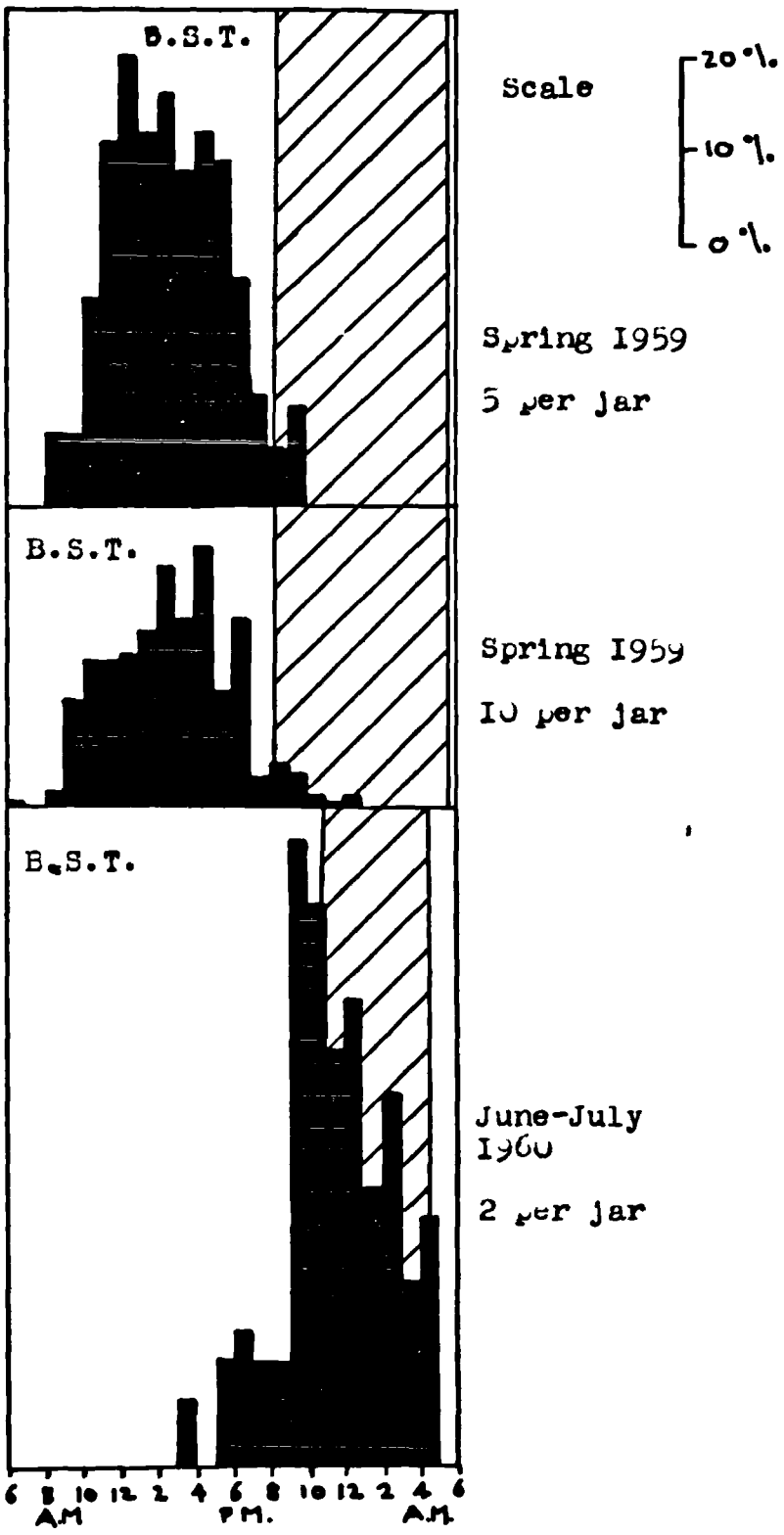
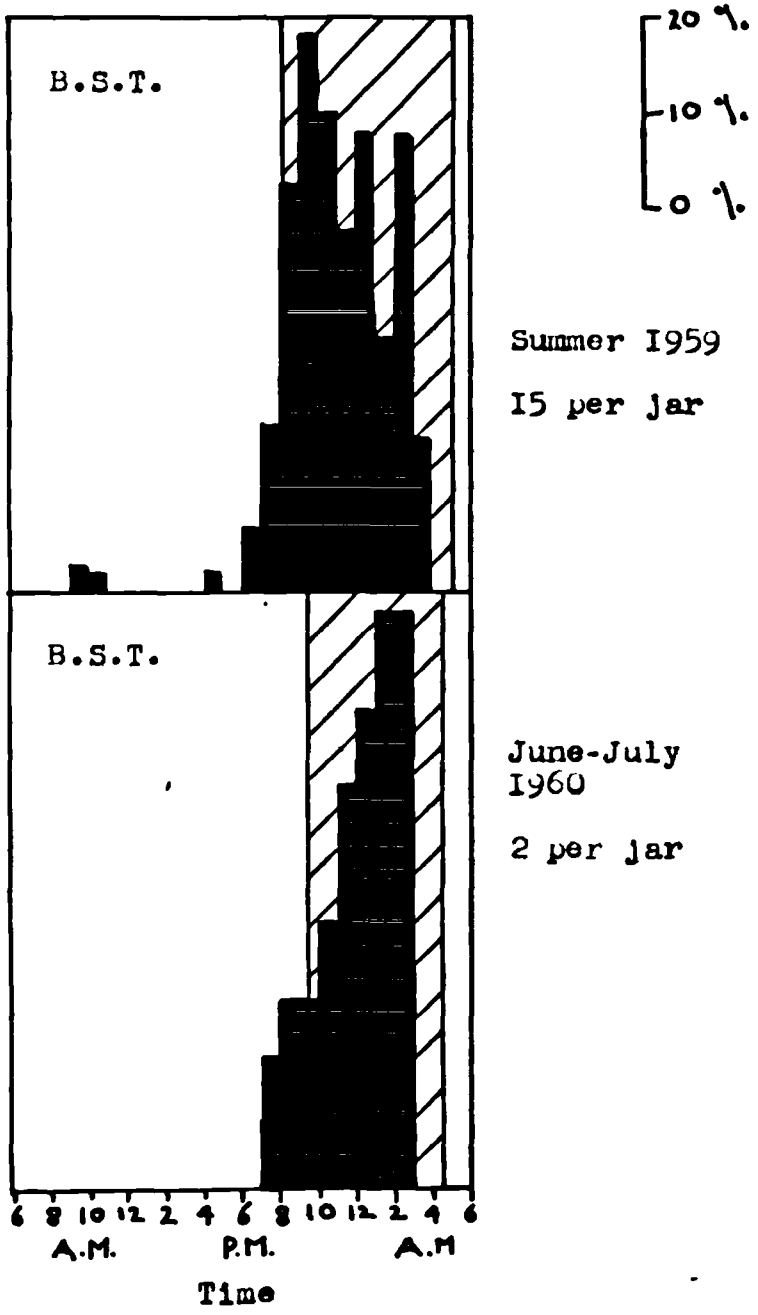

% Activity
B.S.T.
Scale
20 %.
10 %.
0 %.
Asaphidion
Spring 1959
5 per jar
B.S.T.
B.lampros
Spring 1959
10 per jar
B.S.T.
Badister
June-July 1960
2 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M
P.M.
A.M.
Time

Fig.22. % Activity Scale



H.rufipes

Summer 1959

15 per jar

H.affinis

June-July 1960

2 per jar

Fig.23.

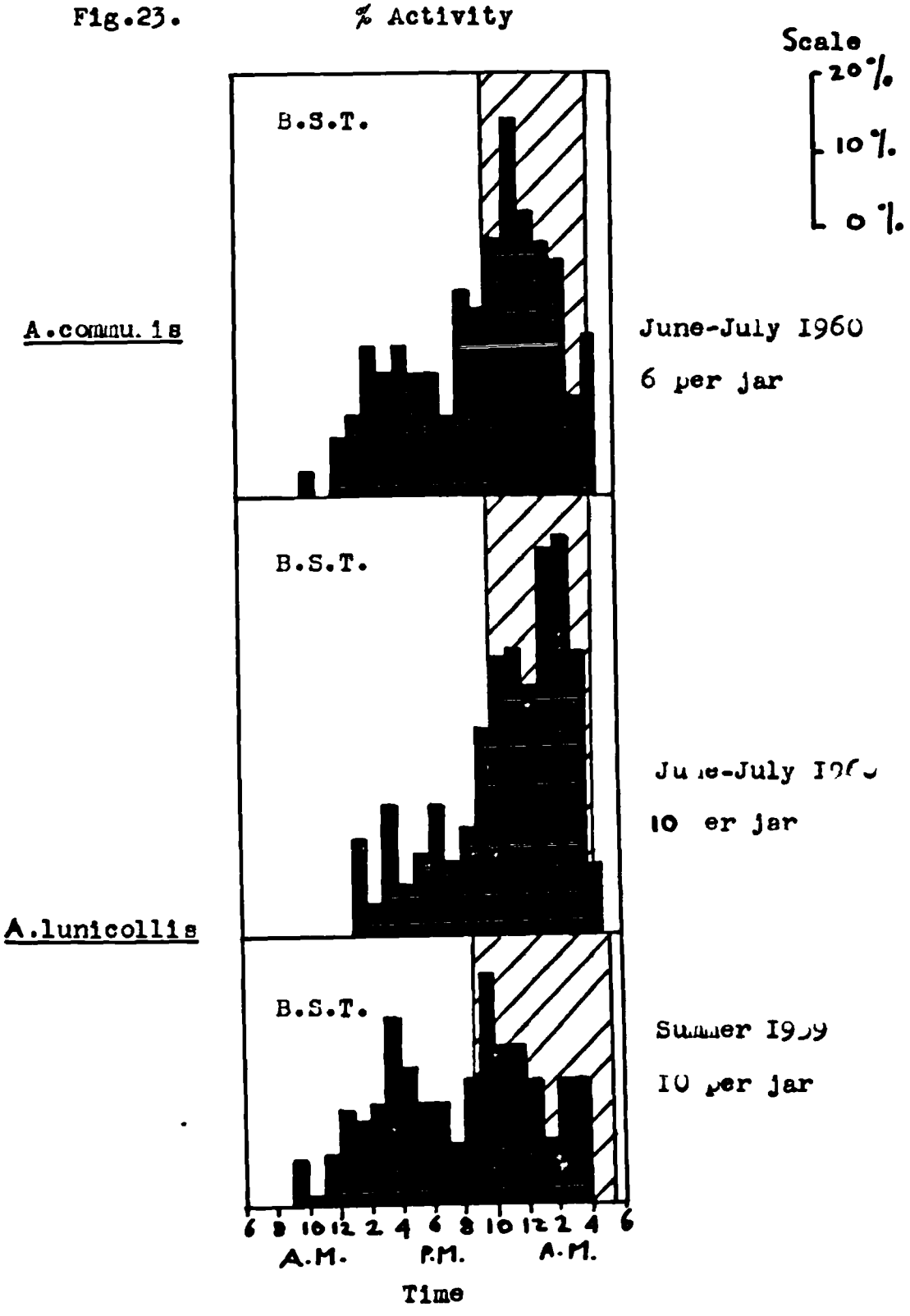

% Activity
Scale
20%.
10%.
0%.
B.S.T.
A.commu. is
June-July 1960
6 per jar
B.S.T.
A.lunicollis
10 er jar
B.S.T.
10 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.24.

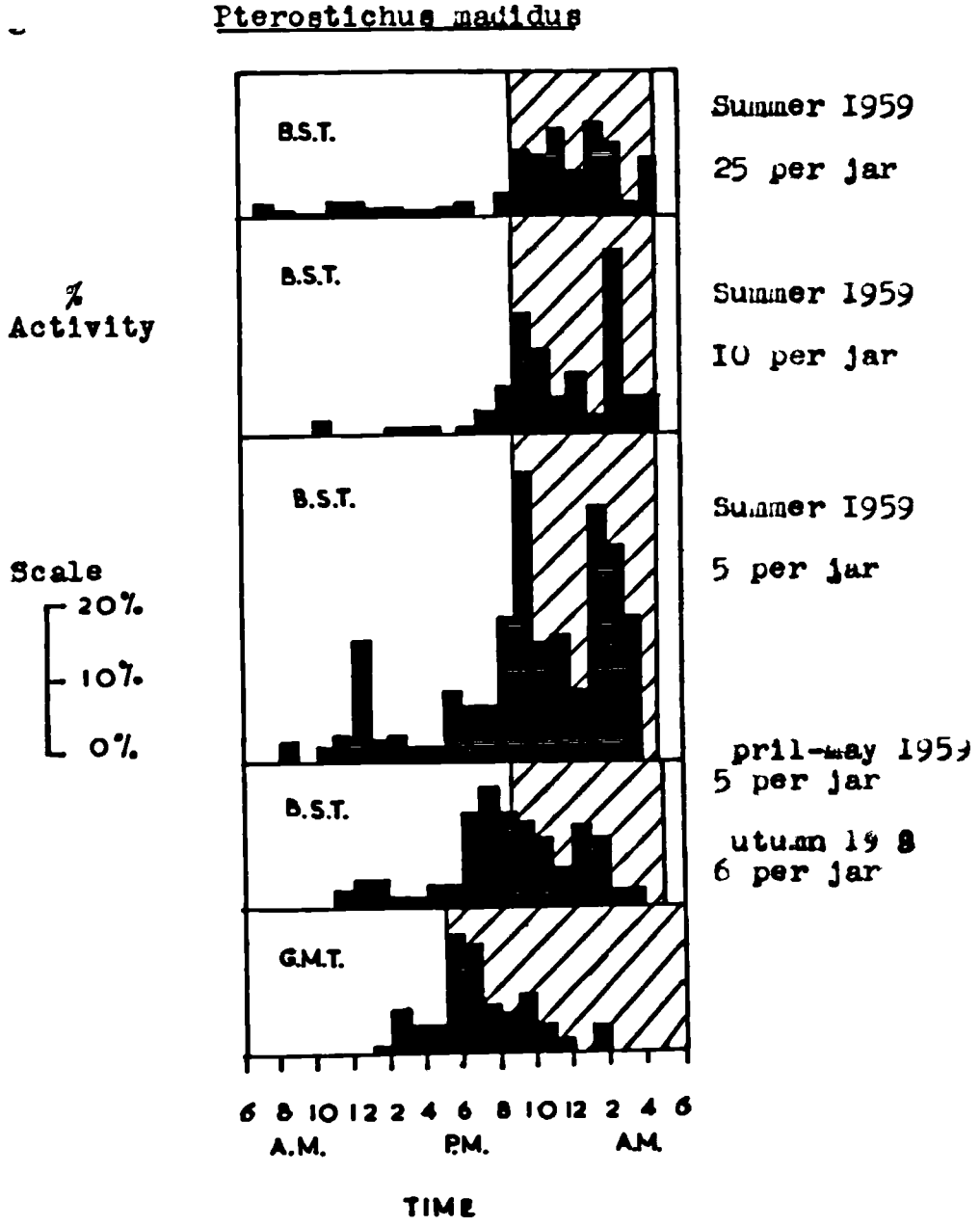

Pterostichus madidus
B.S.T.
Summer 1959
25 per jar
B.S.T.
Summer 1959
10 per jar
% Activity
B.S.T.
Summer 1959
5 per jar
Scale
20%
10%
0%
pril-May 1959
5 per jar
B.S.T.
utumn 19 8
6 per jar
G.M.T.
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
TIME

Fig.25.

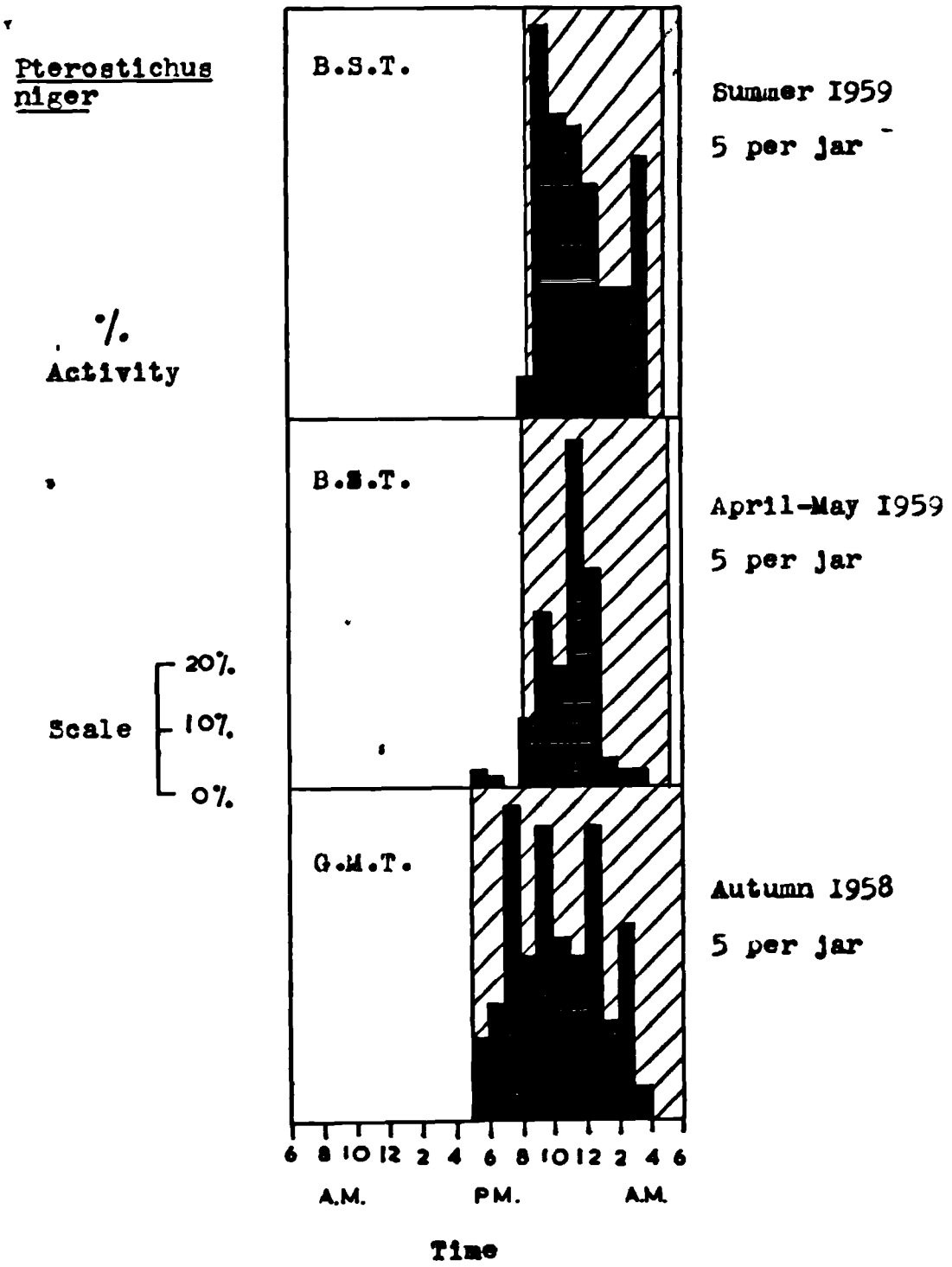

Pterostichus niger
B.S.T.
Summer 1959
5 per jar
%
Activity
B.S.T.
April-May 1959
5 per jar
Scale
20%
10%
0%
G.M.T.
Autumn 1958
5 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.26.

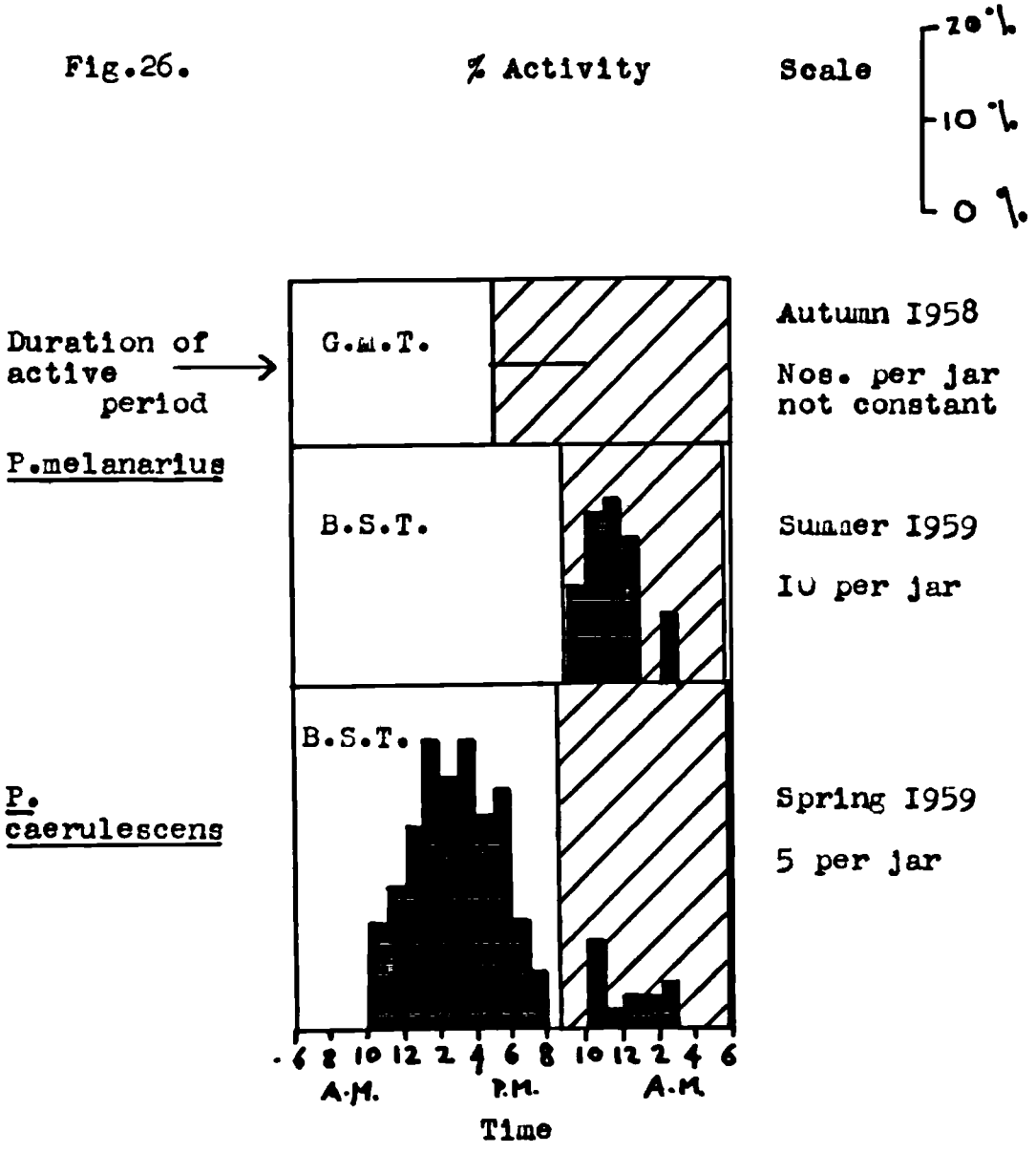

% Activity
Scale
20 %
10 %
0 %
Duration of active period
G.M.T.
Autumn 1958
Nos. per jar not constant
P.melanarius
B.S.T.
Summer 1959
10 per jar
B.S.T.
P. caerulescens
Spring 1959
5 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.27.

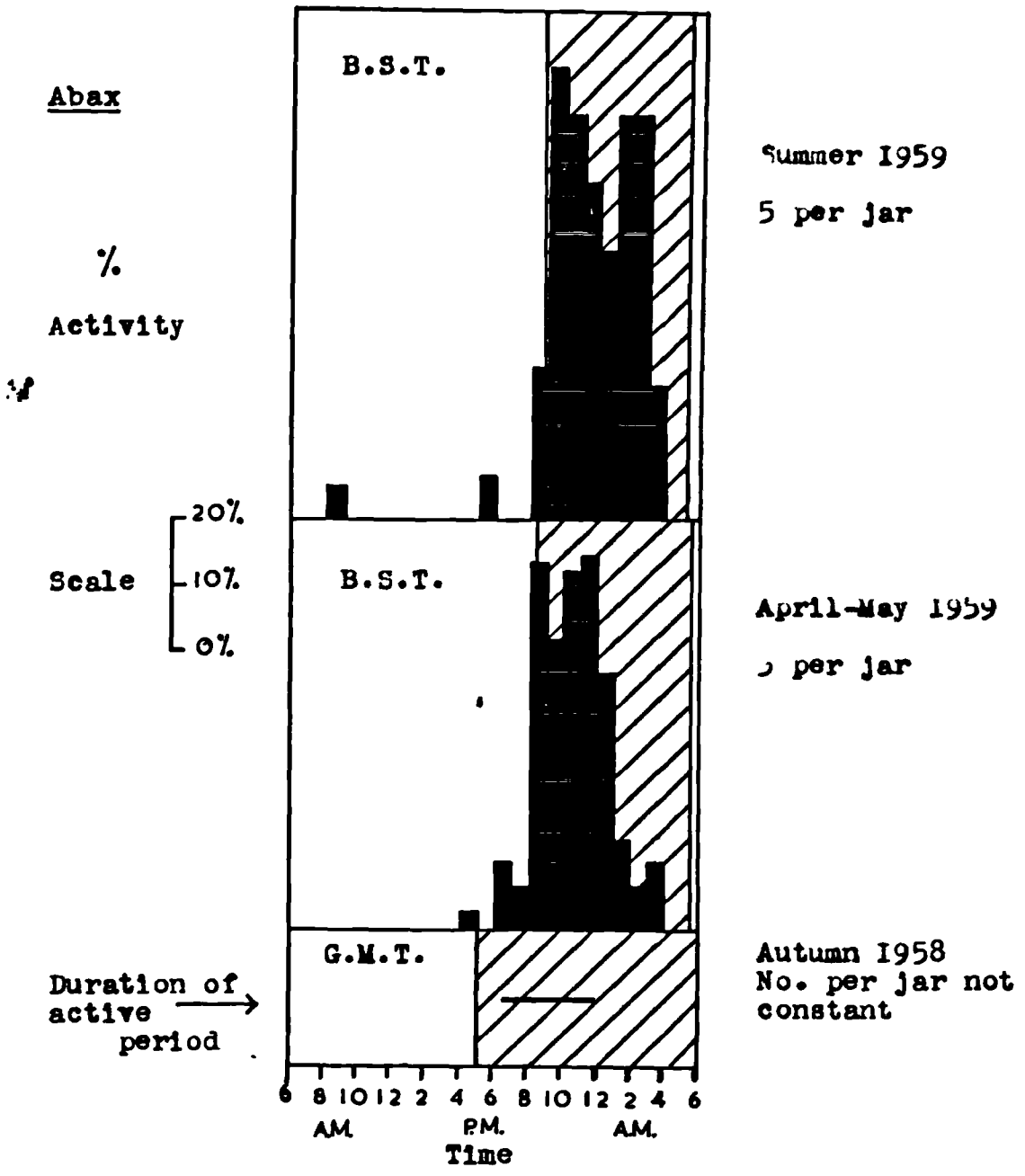
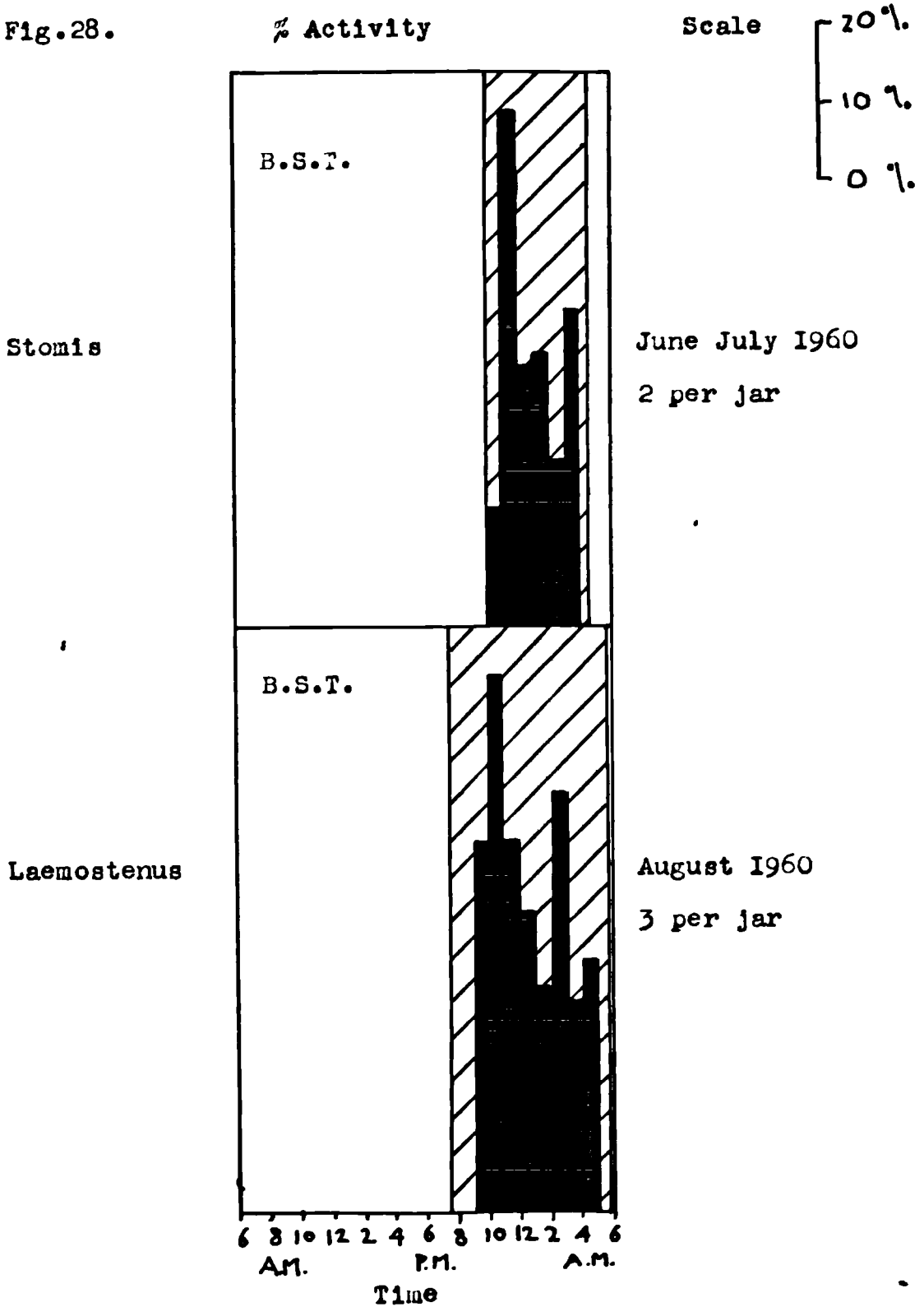

Abax
%
Activity
B.S.T.
Summer 1959
5 per jar
Scale
20%
10%
0%
B.S.T.
April-May 1959
5 per jar
G.M.T.
Autumn 1958
No. per jar not constant
Duration of active period
6 8 10 12 2 4 6 8 10 12 2 4 6
AM.
P.M.
A.M.
Time

Fig.28.


% Activity
Scale
20 %.
10 %.
0 %.
B.S.T.
Stomis
June July 1960
2 per jar
B.S.T.
Laemostenus
August 1960
3 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

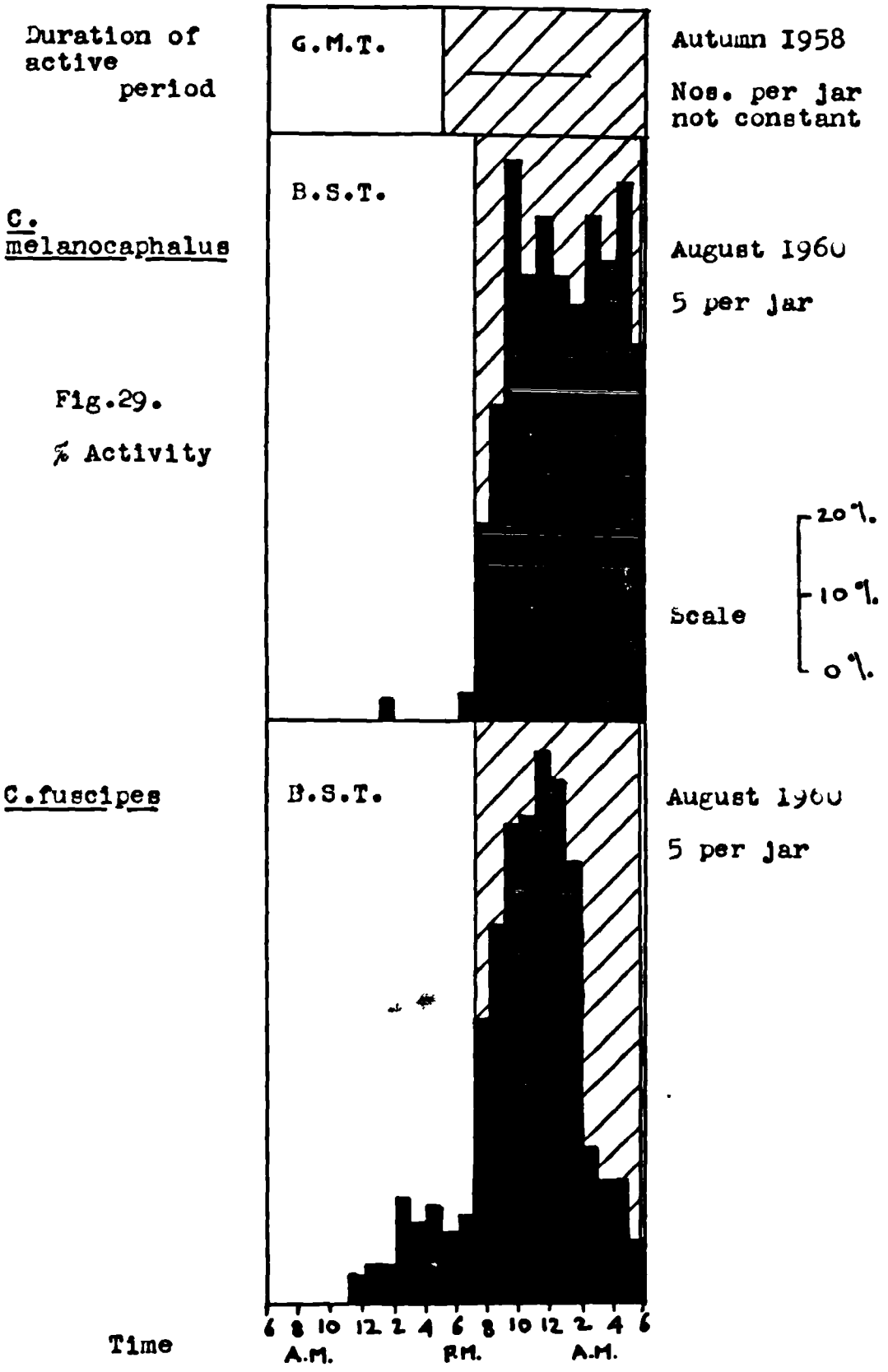

Duration of active period
G.M.T.
B.S.T.
Autumn 1958
Nos. per jar not constant
C. melanocaphalus
August 1960
5 per jar
% Activity
20%.
10%.
0%.
Scale
C.fuscipes
B.S.T.
August 1960
5 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.29.

Fig.30.

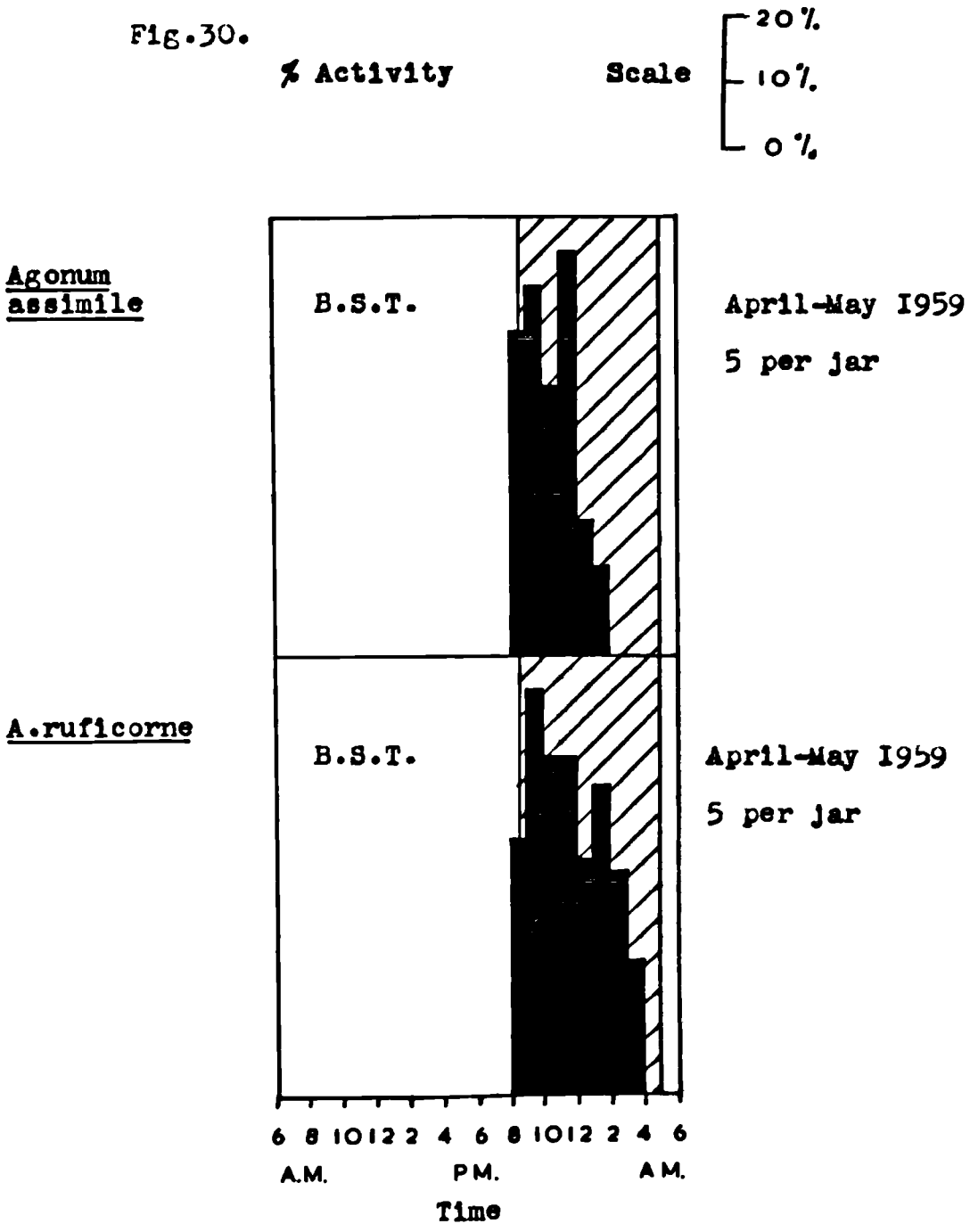

% Activity
Scale
20%
10%
0%
Agonum assimile
B.S.T.
April-May 1959
5 per jar
A.ruficorne
B.S.T.
April-May 1959
5 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A.M.
Time

Fig.31.

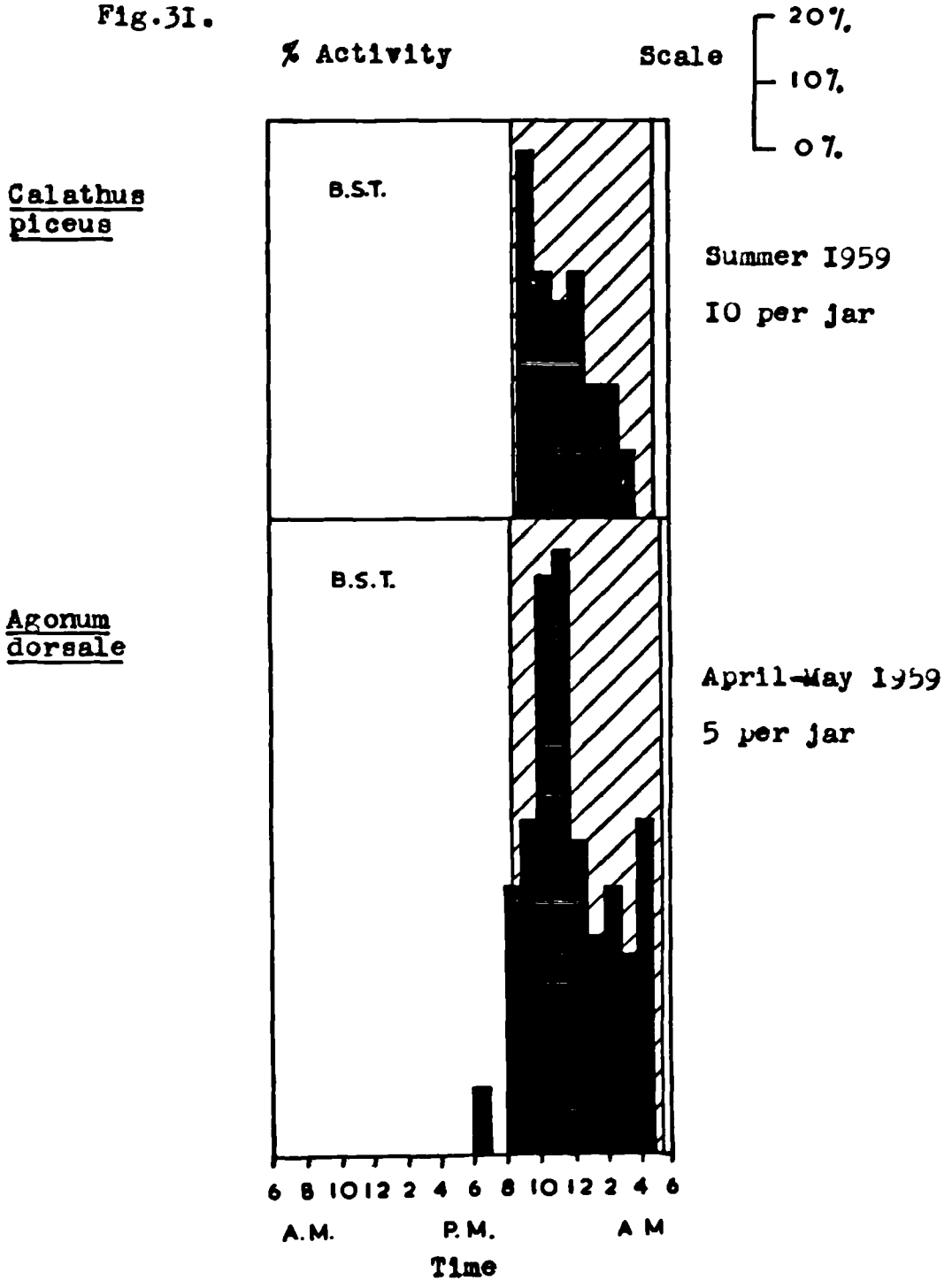

% Activity
Scale
20%.
10%.
0%.
Calathus piceus
B.S.T.
Summer 1959
10 per jar
Agonum dorsale
B.S.T.
April-May 1959
5 per jar
6 8 10 12 2 4 6 8 10 12 2 4 6
A.M.
P.M.
A M
Time

Fig.32.

Annual distribution of activity in Diurnal and Nocturnal Carabidae.

Catch of 23 permanent traps - Oct.1958-Oct.1959

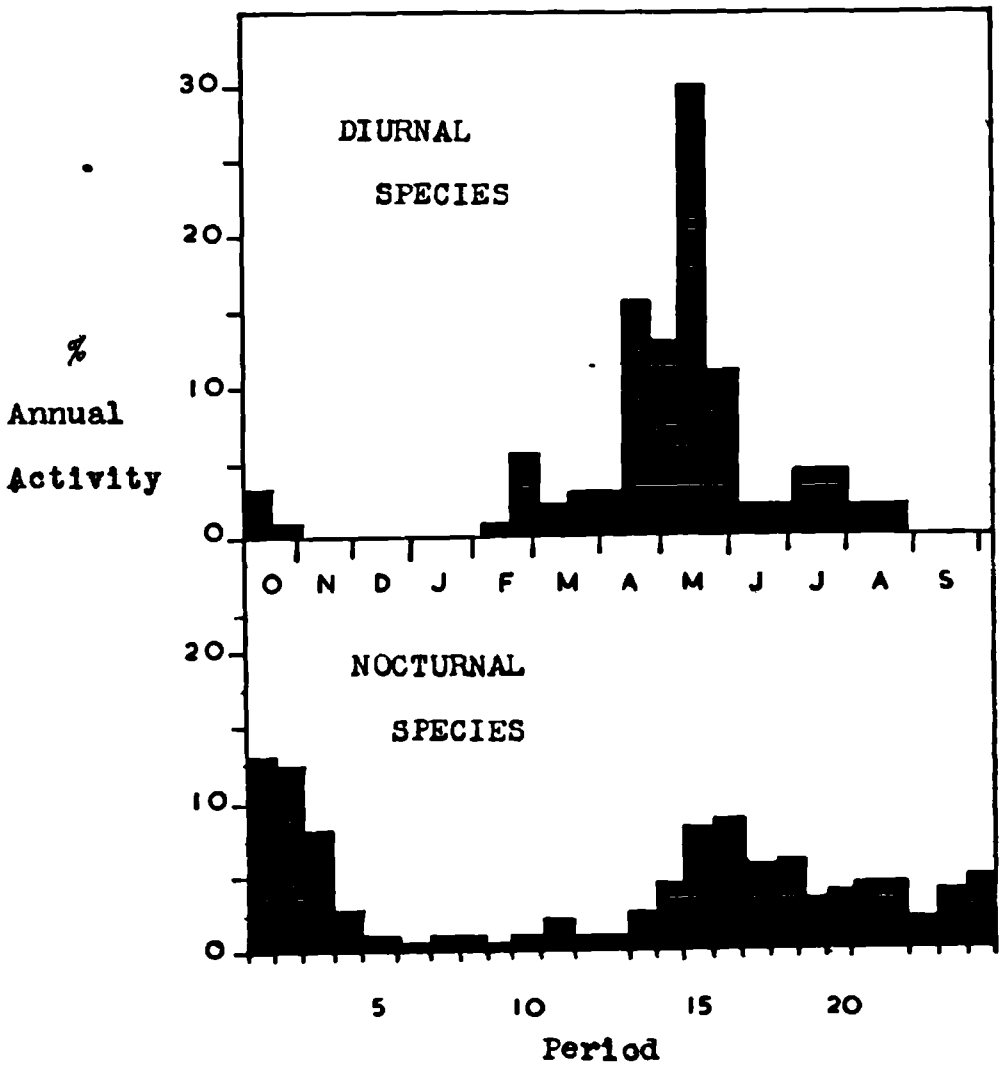


Fig.33.

Rate of loss of marks in an insectary culture of P.madidus (♂♂)

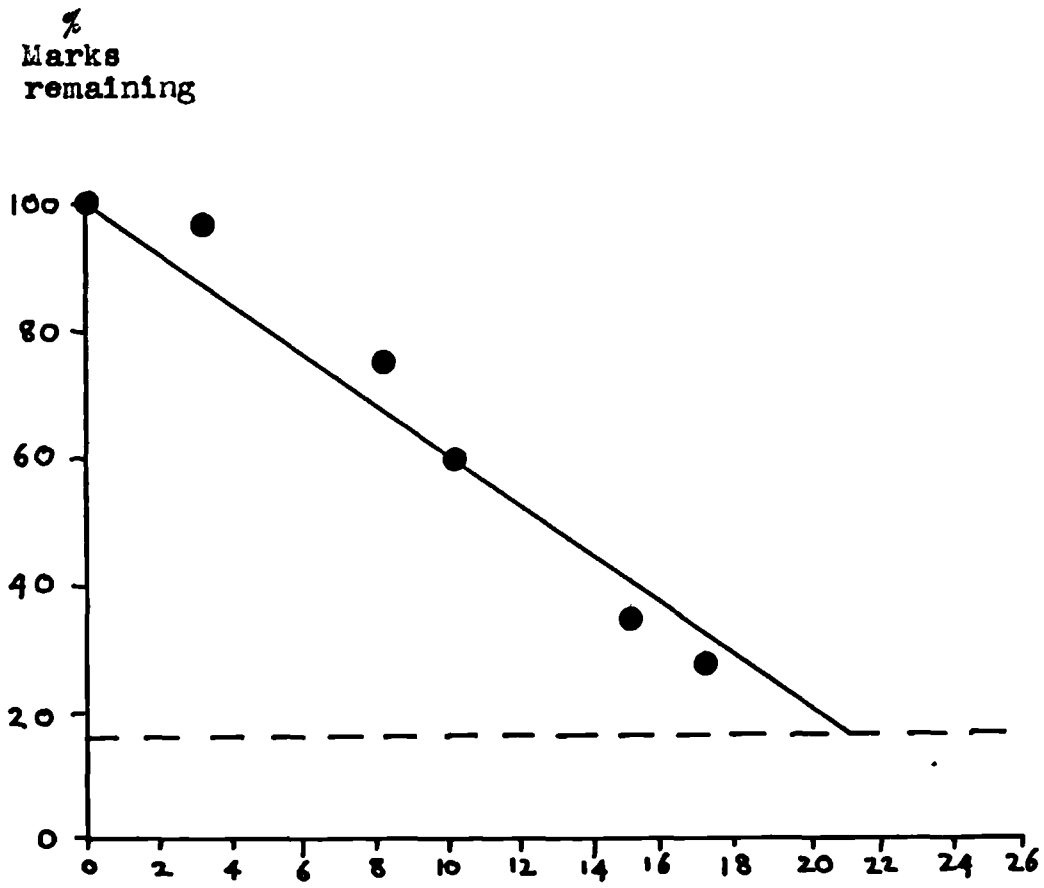


Fig.34.

Rate of loss of marks in the field in P.madidus (both sexes)

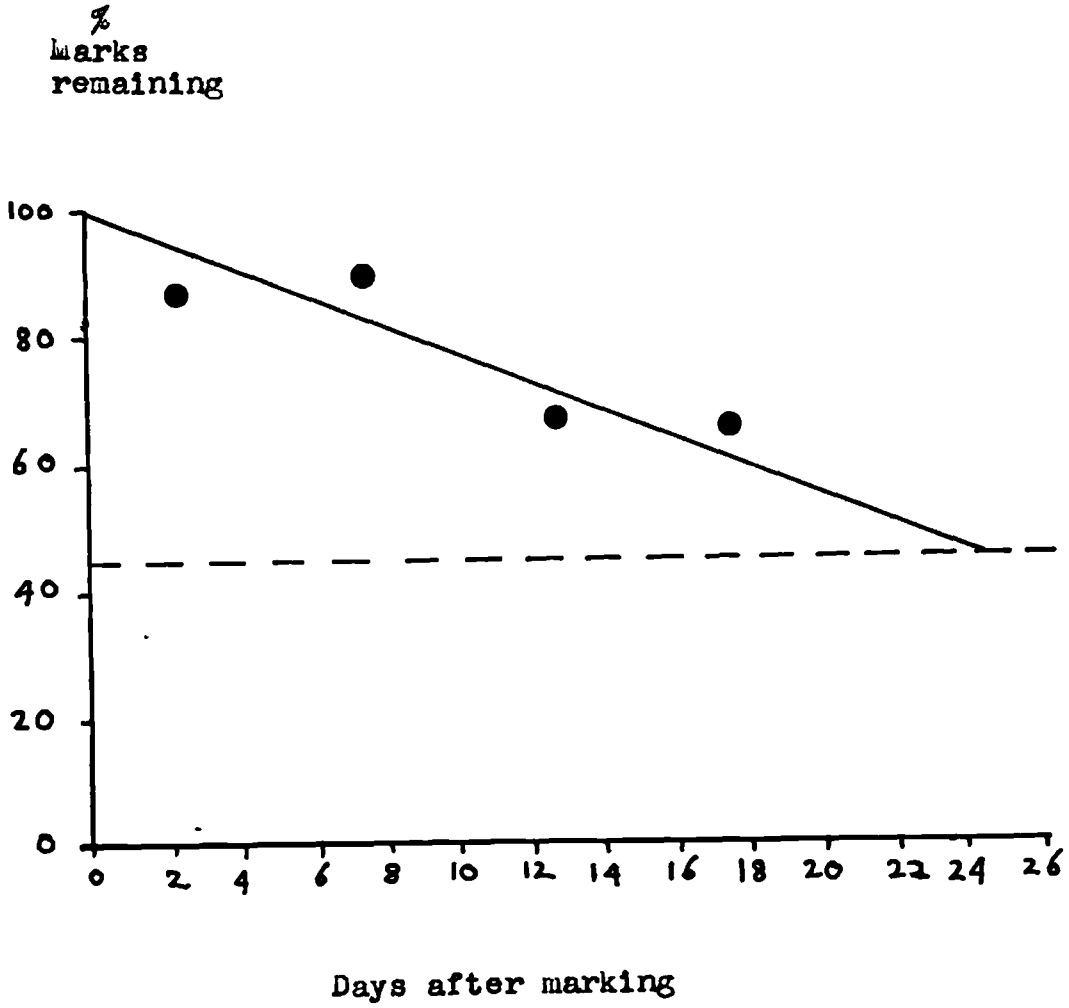
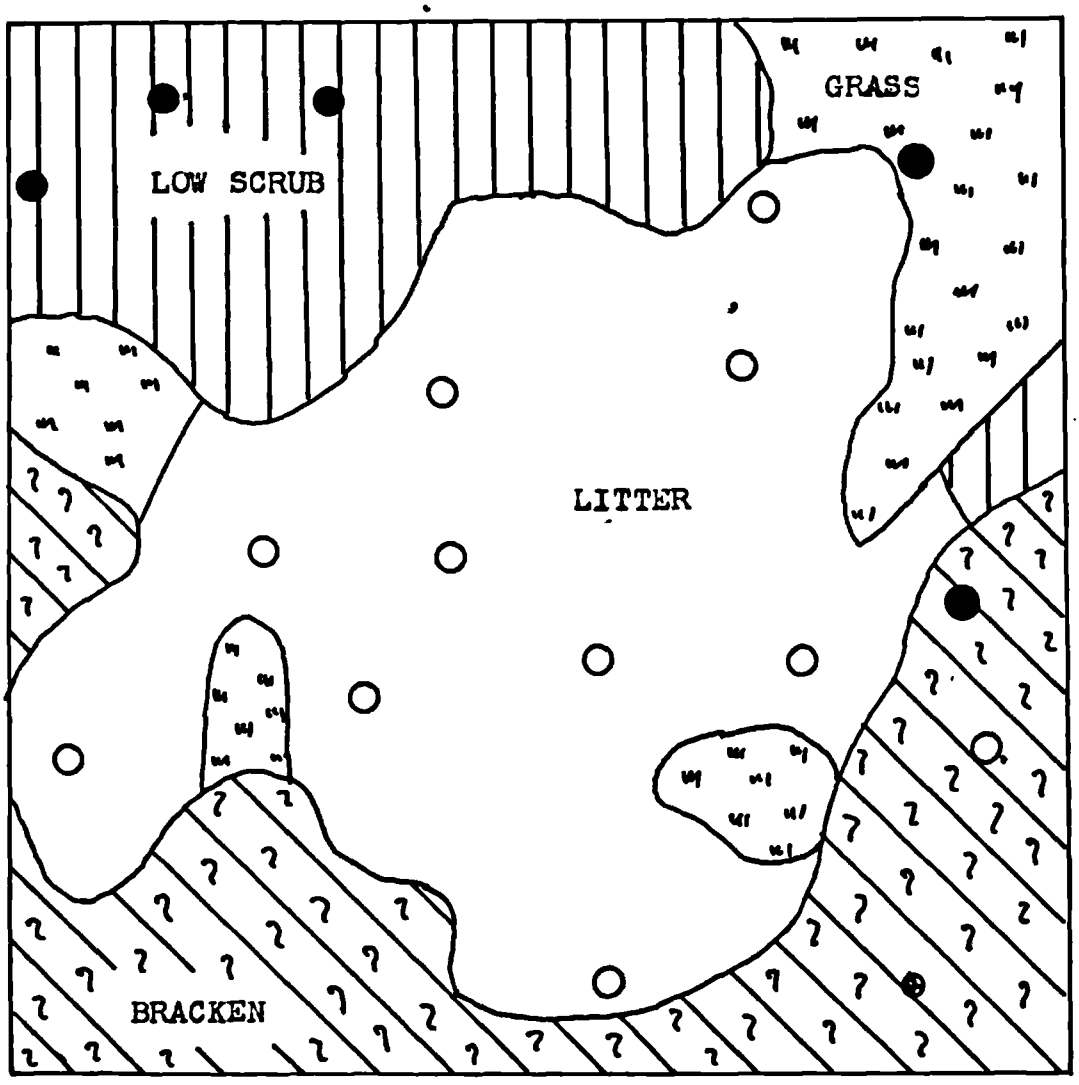


Fig.35.

Vegetation of Wood Bank beech litter plot. 1960.

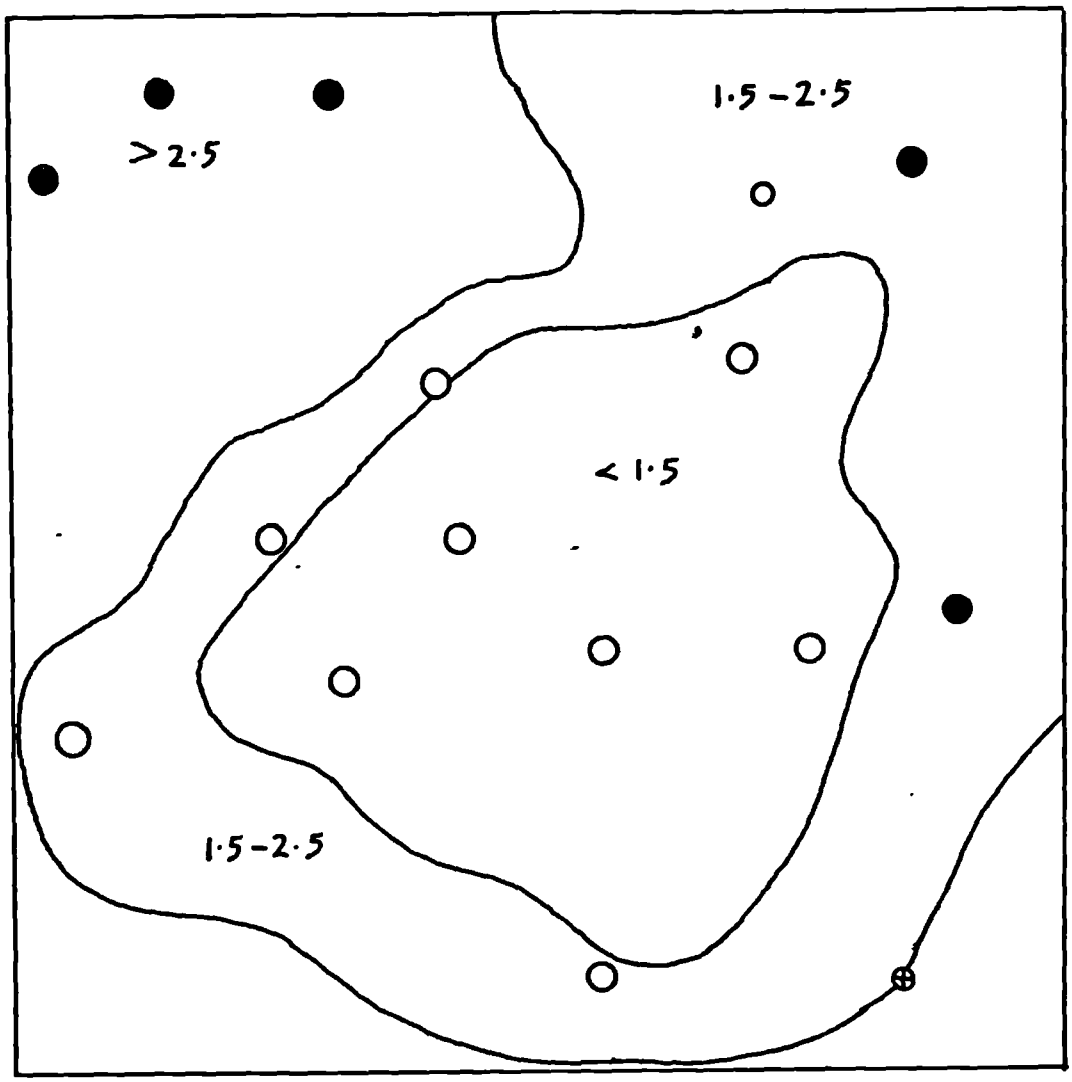


Tree species : ● Oak ; ○ Beech ; ⊛ Pinus

Scale 10 yds.

Fig.36.

Litter depths (inches) - Wood Bank beech litter plot 1960

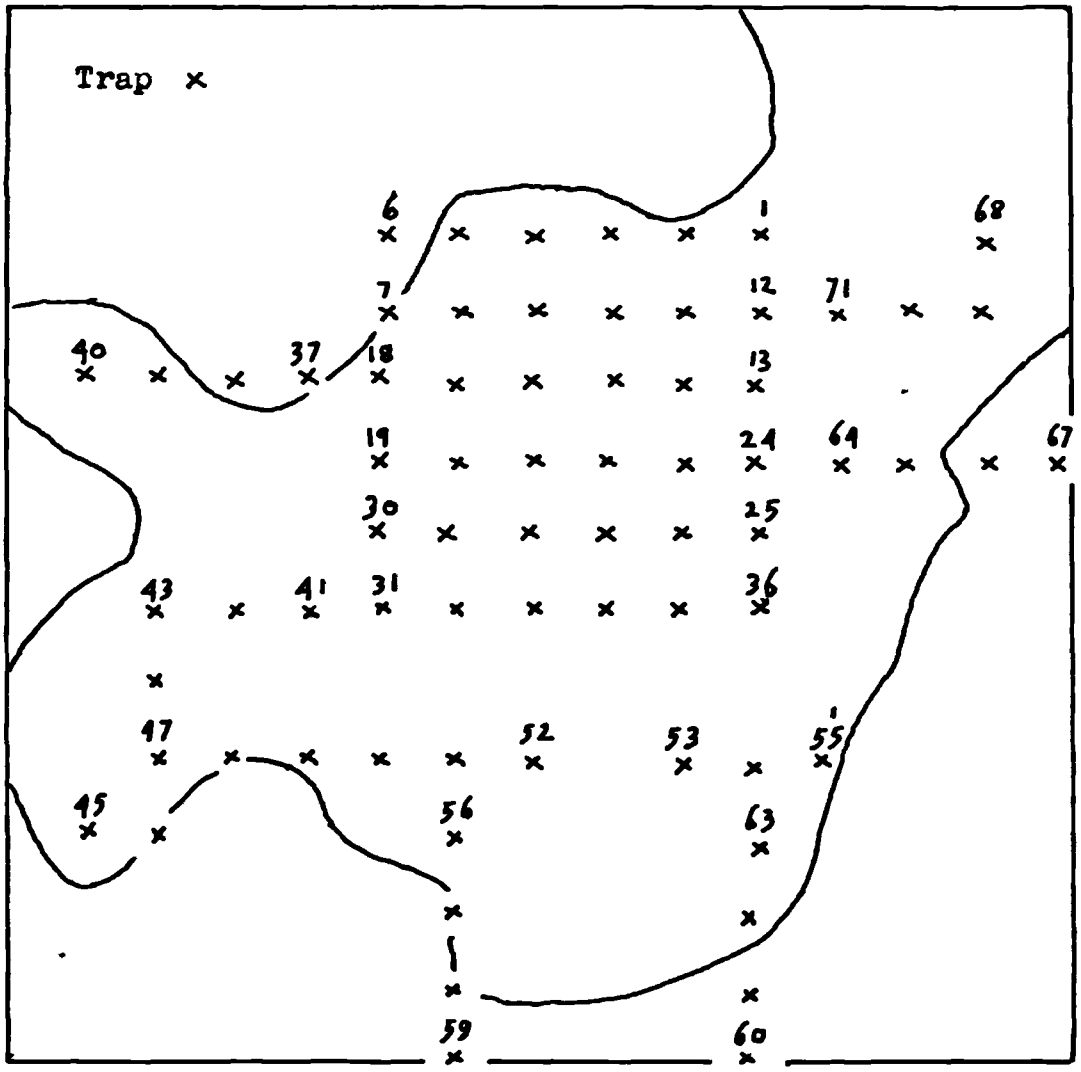


Scale and tree species as Fig.35.

Fig.37.

Distribution of traps - Wood Bank plot

(a) 1959



Limits of bracken and scrub areas are shown.

Fig.37. (Continued)

Distribution of traps - Wood Bank plot

(b) 1960

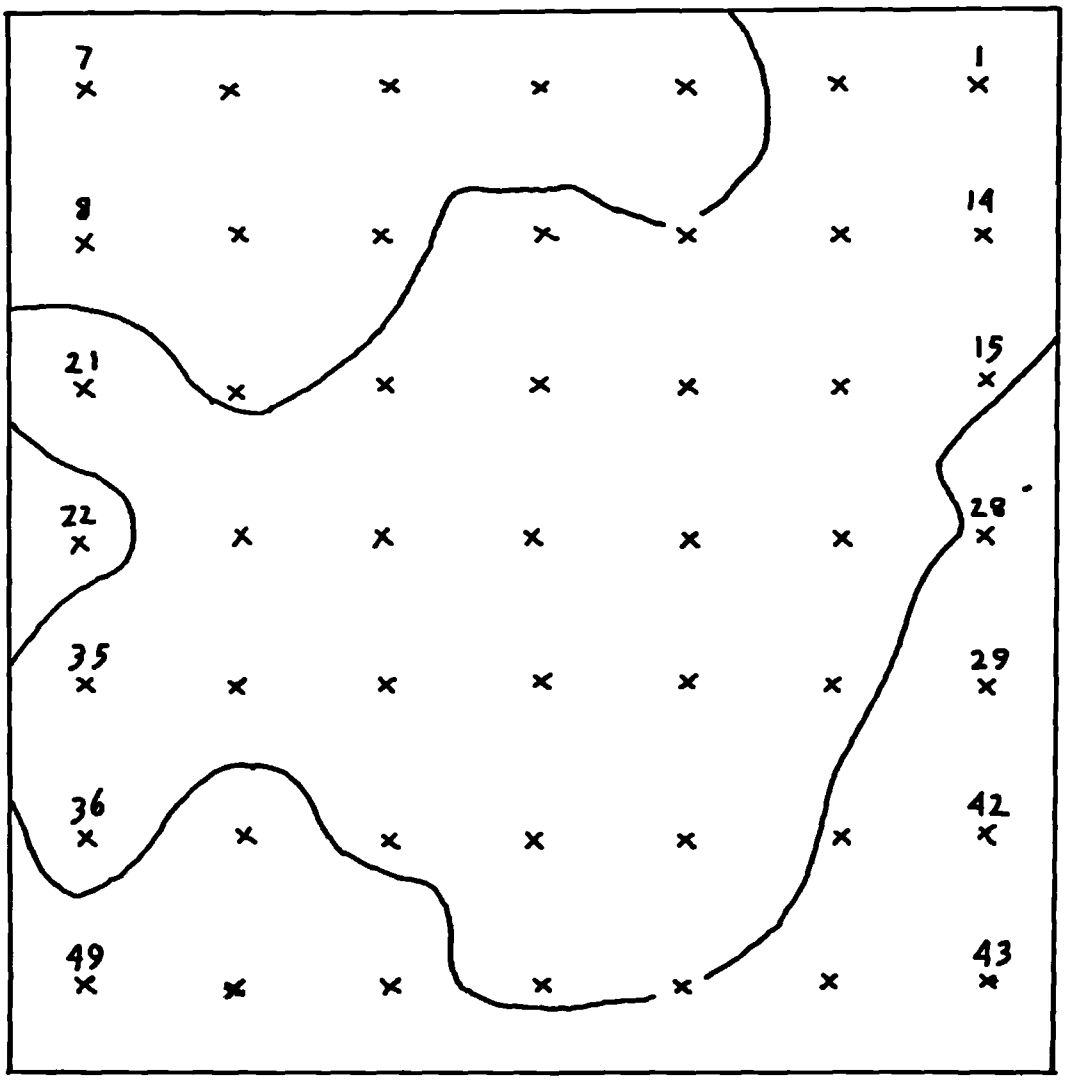
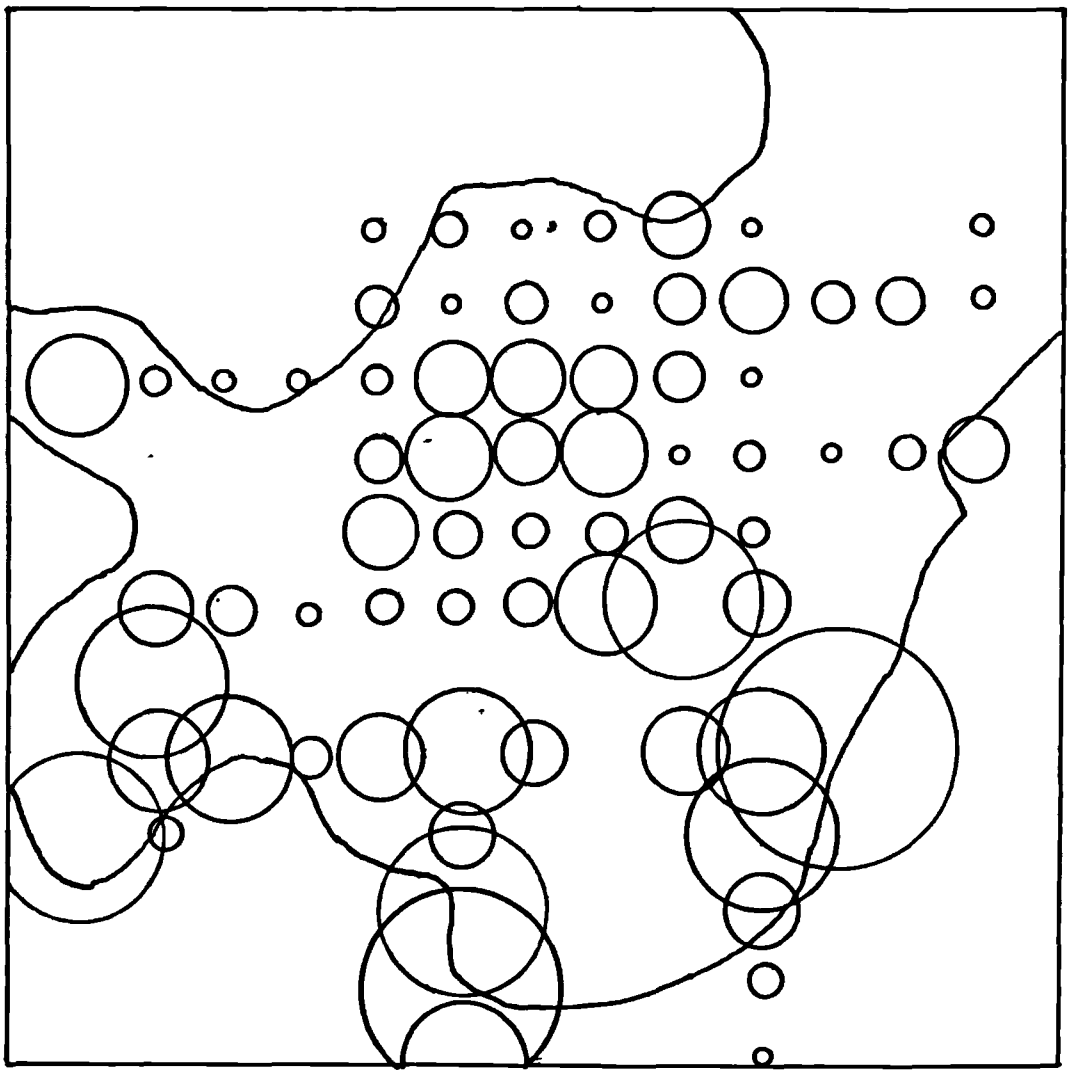


Fig.38.

Catches of N.brevicollis — Wood Bank plot
Autumn 1959

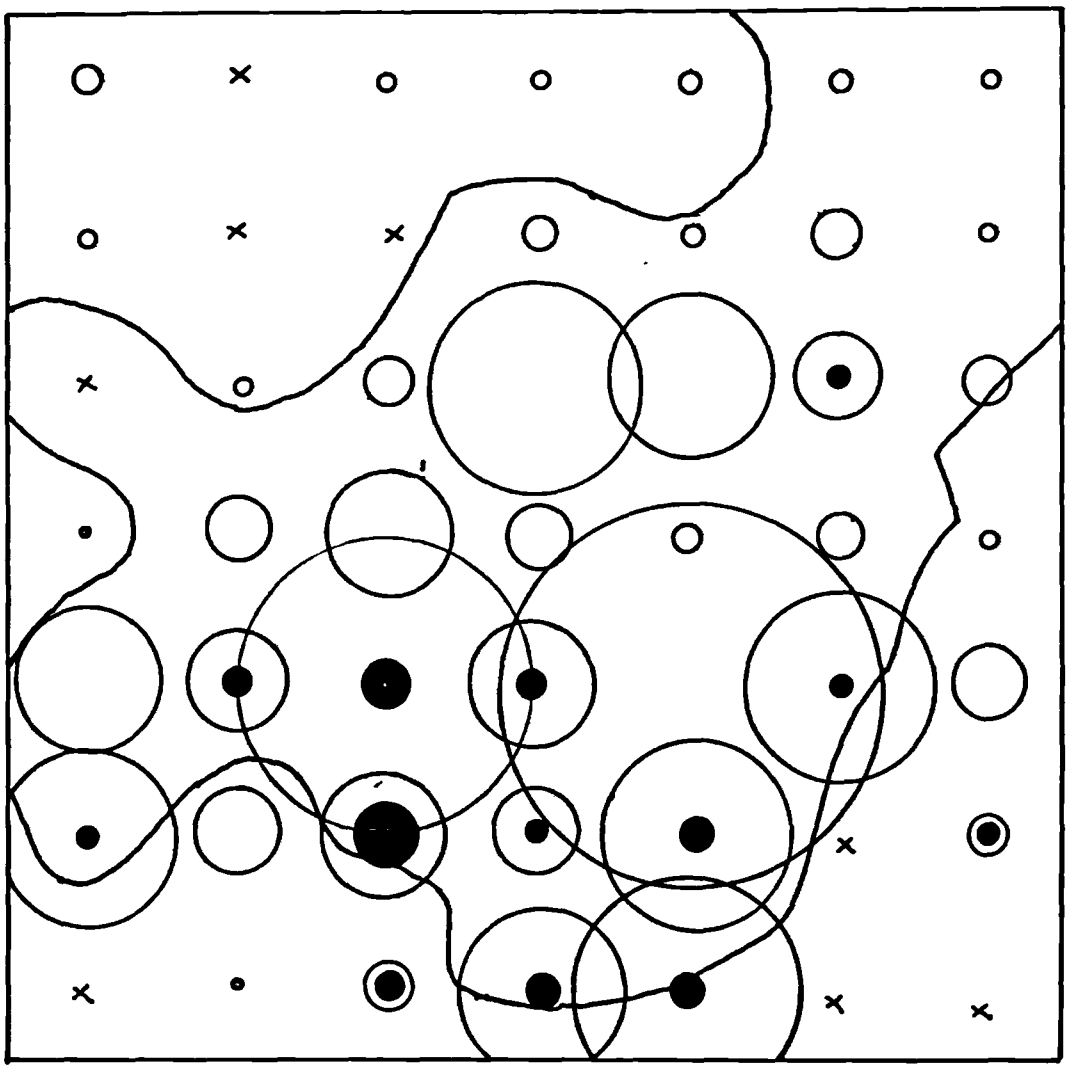


Scale :



Fig.39.

Total catches of N.brevicollis on Wood Bank plot 1960.
Including callows.



Scale :

× 0 • 1 10 20 Callows

Fig.40.

Marked Nebria (as % of total catch) in three zones of Wood Bank plot, according to time after release. Autumn 1959.

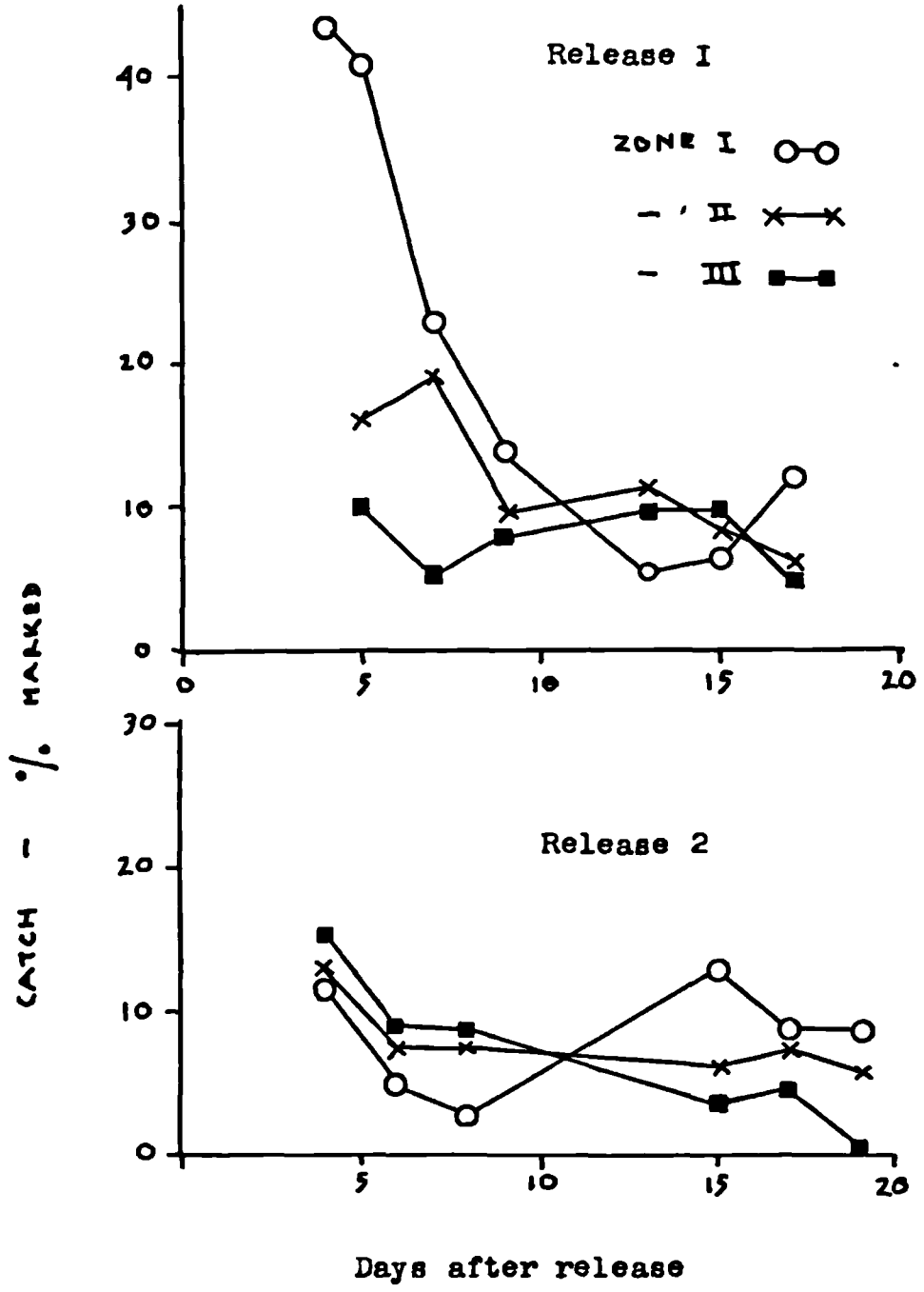


Fig.40. (Continued)

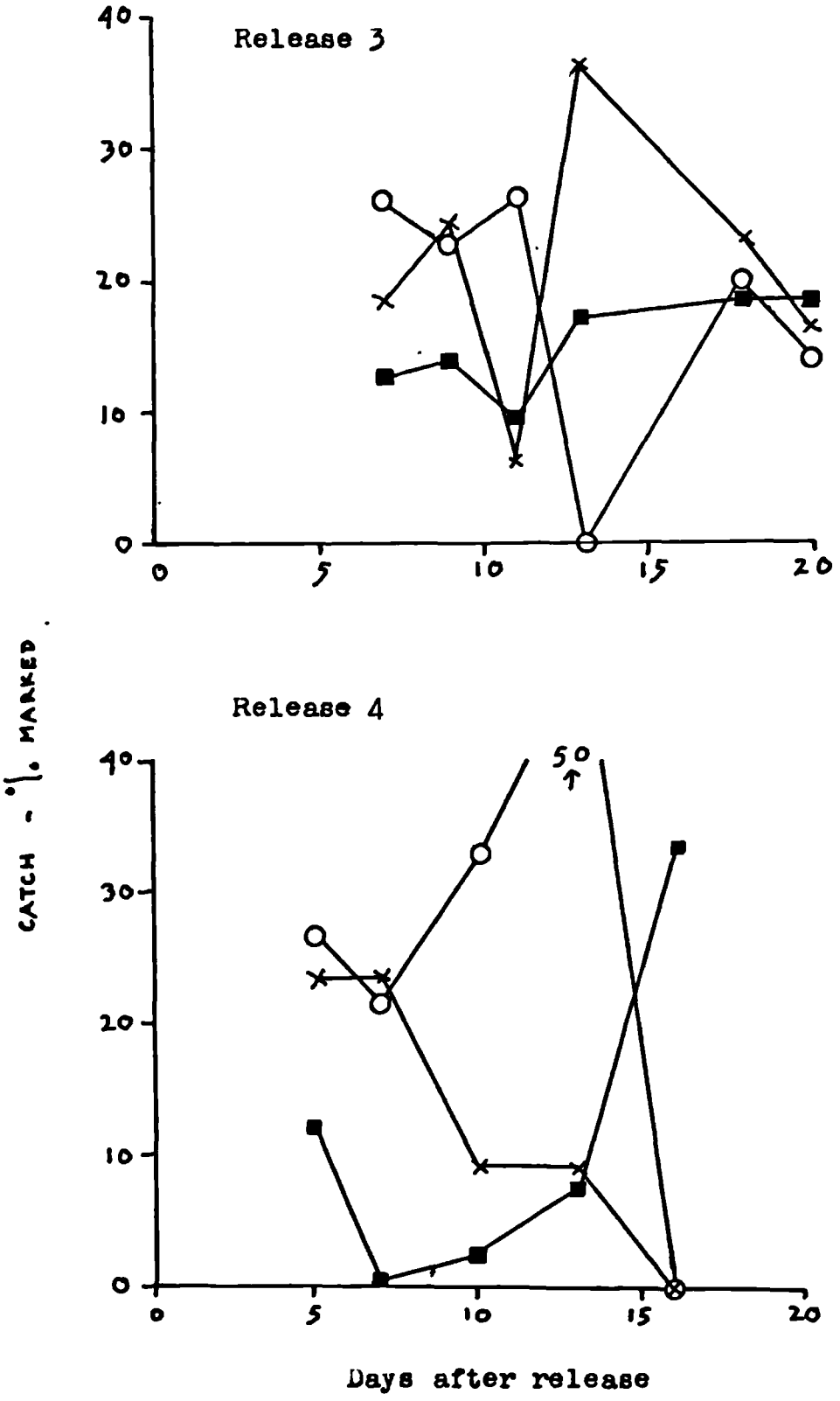
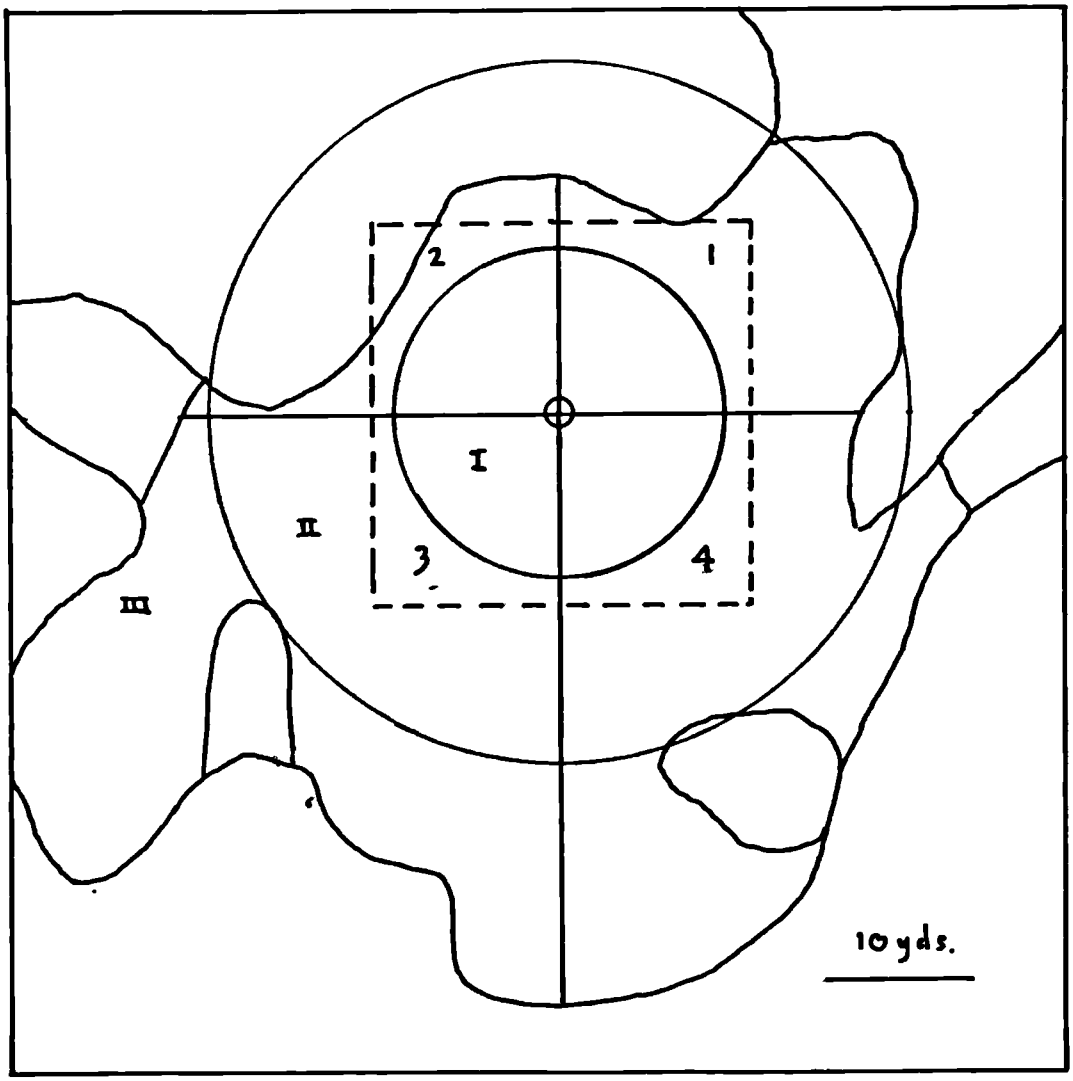


Fig.4I.

Wood Bank plot - Limits of vegetation types, zones and sectors, 1959.

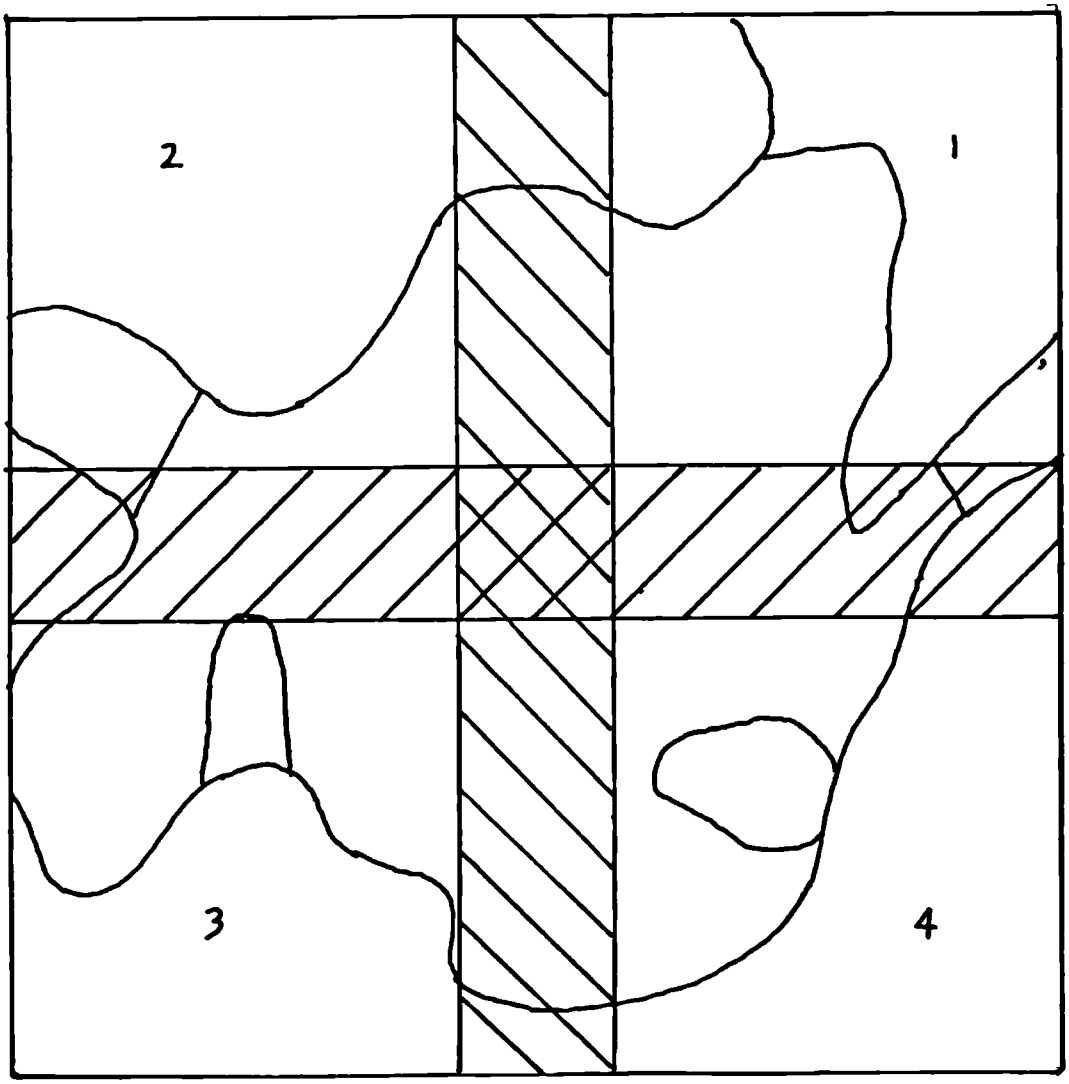


O Release point
I - III Zones
1 — 4 Sectors
Broken line - Boundary of main trap system

Fig.42.

Limits of vegetation types and sectors.
Wood Bank plot - 1960

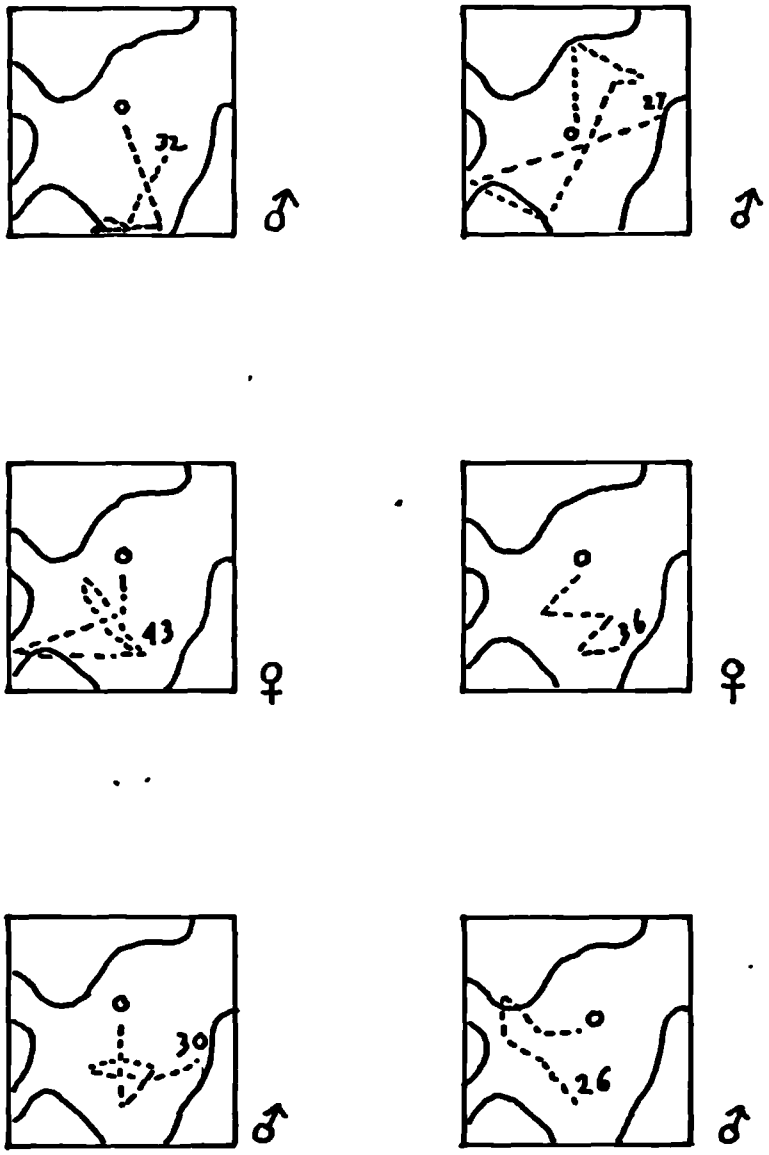
Areas common to 2 or more sectors shown hatched.



1-4 Sectors

Fig.43.

Examples of movement of marked Nebria.
Wood Bank, Autumn 1960.



Limits of bracken and scrub are shown, and also no. of days between release and final recapture.

Fig.44.

Nebria recaptures as % of total catch, according to time after release. Wood Bank plot . Autumn 1959.

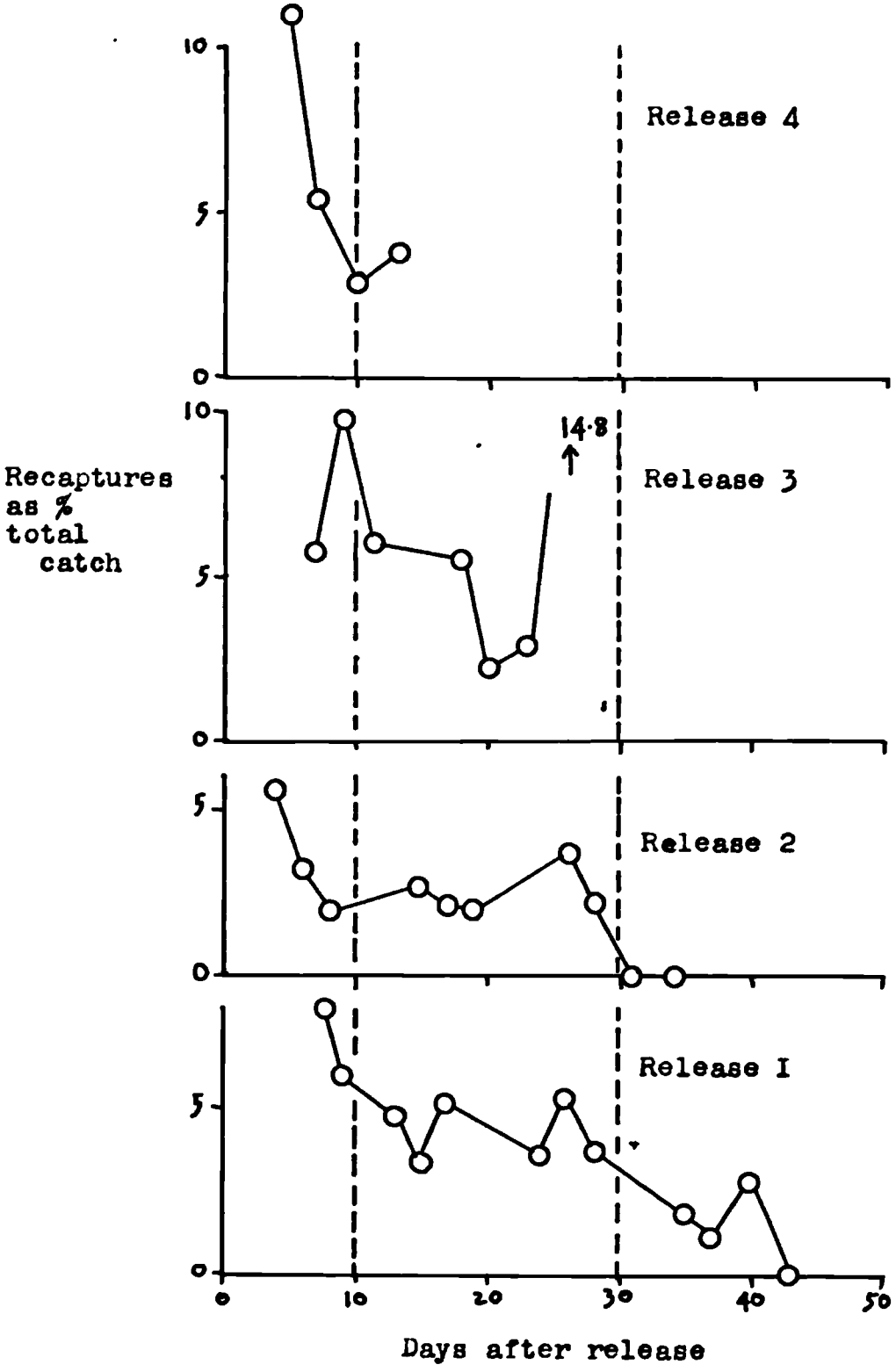


Fig.45.

Recaptures of Nebria as % of total catch Autumn 1960. Wood Bank plot.

(2-point running-means are plotted against time after release)

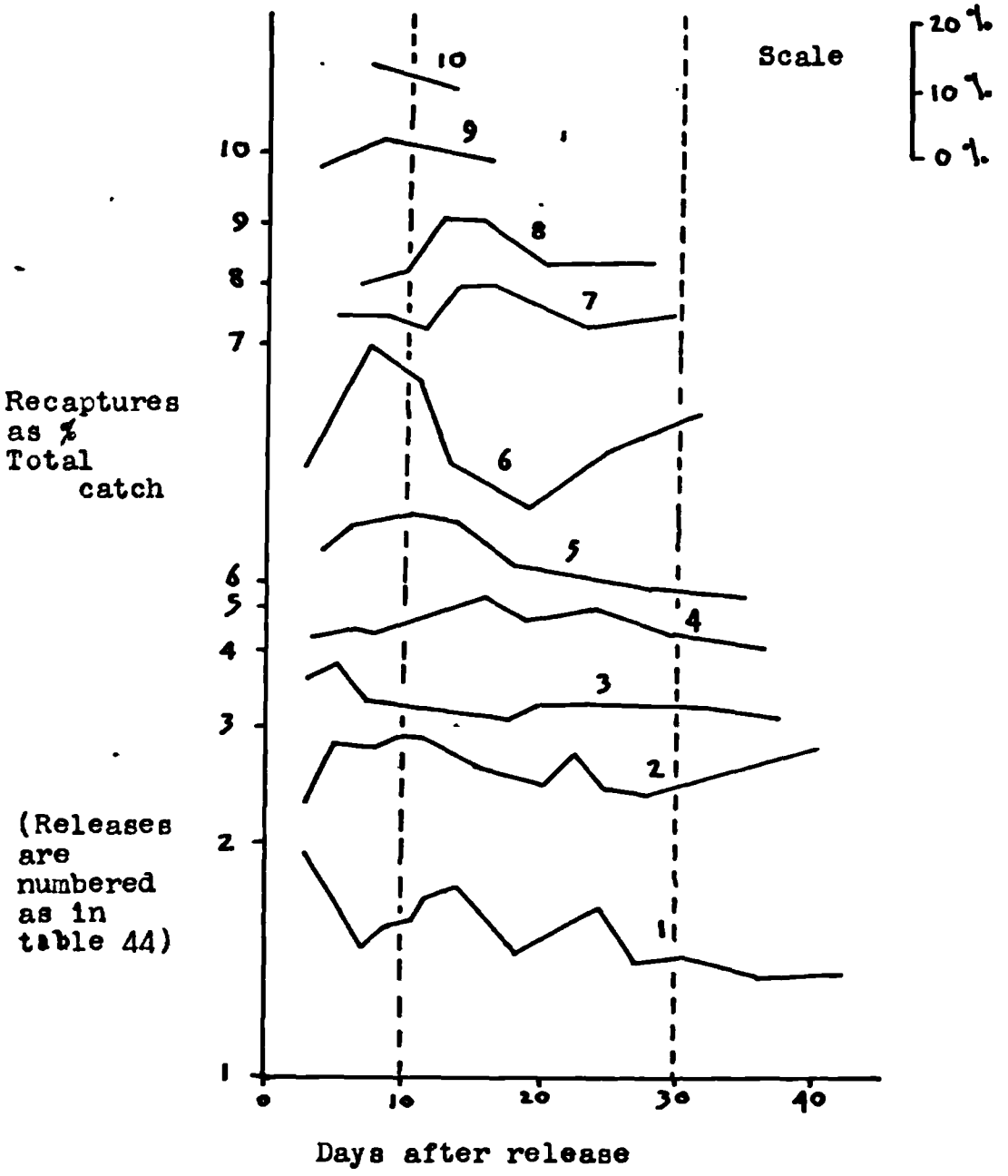


Fig.46.

% of catch of N.brevicollis found to be marked - Wood Bank plot Autumn 1960.
All releases included.

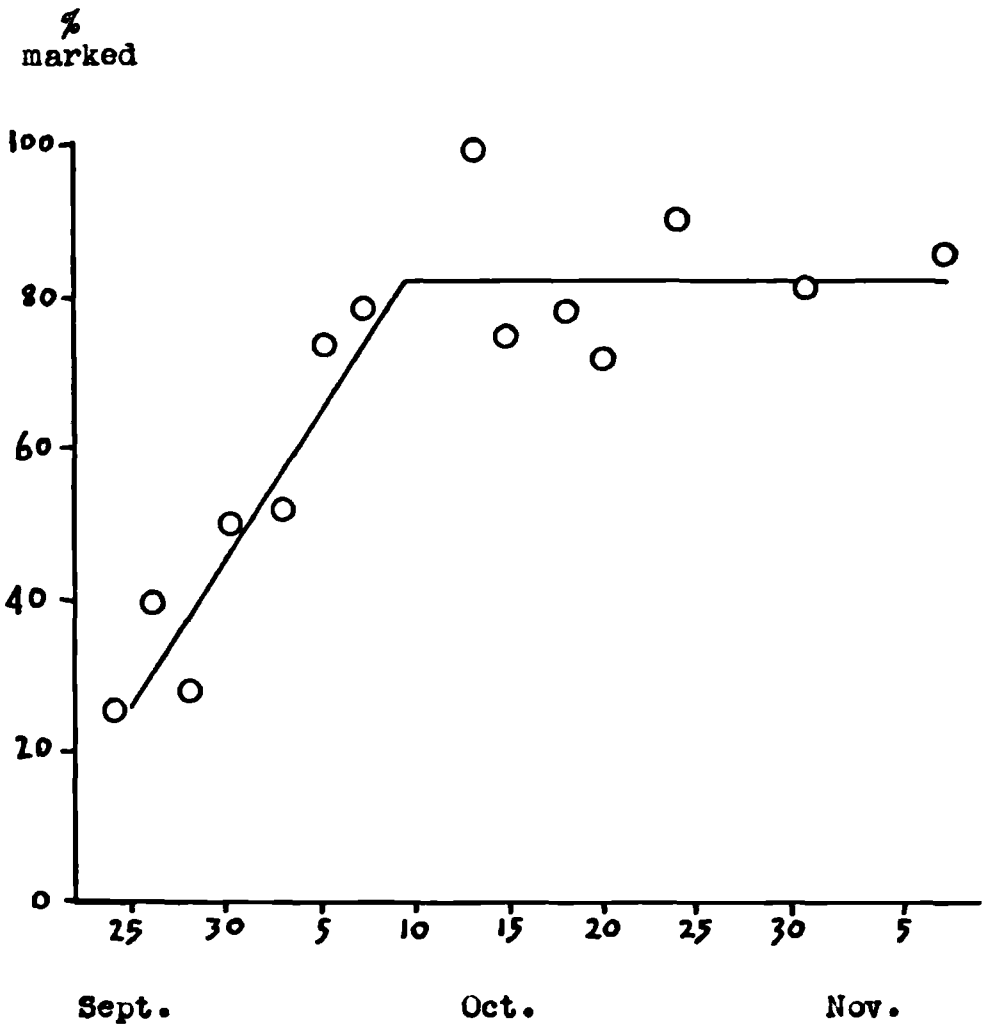
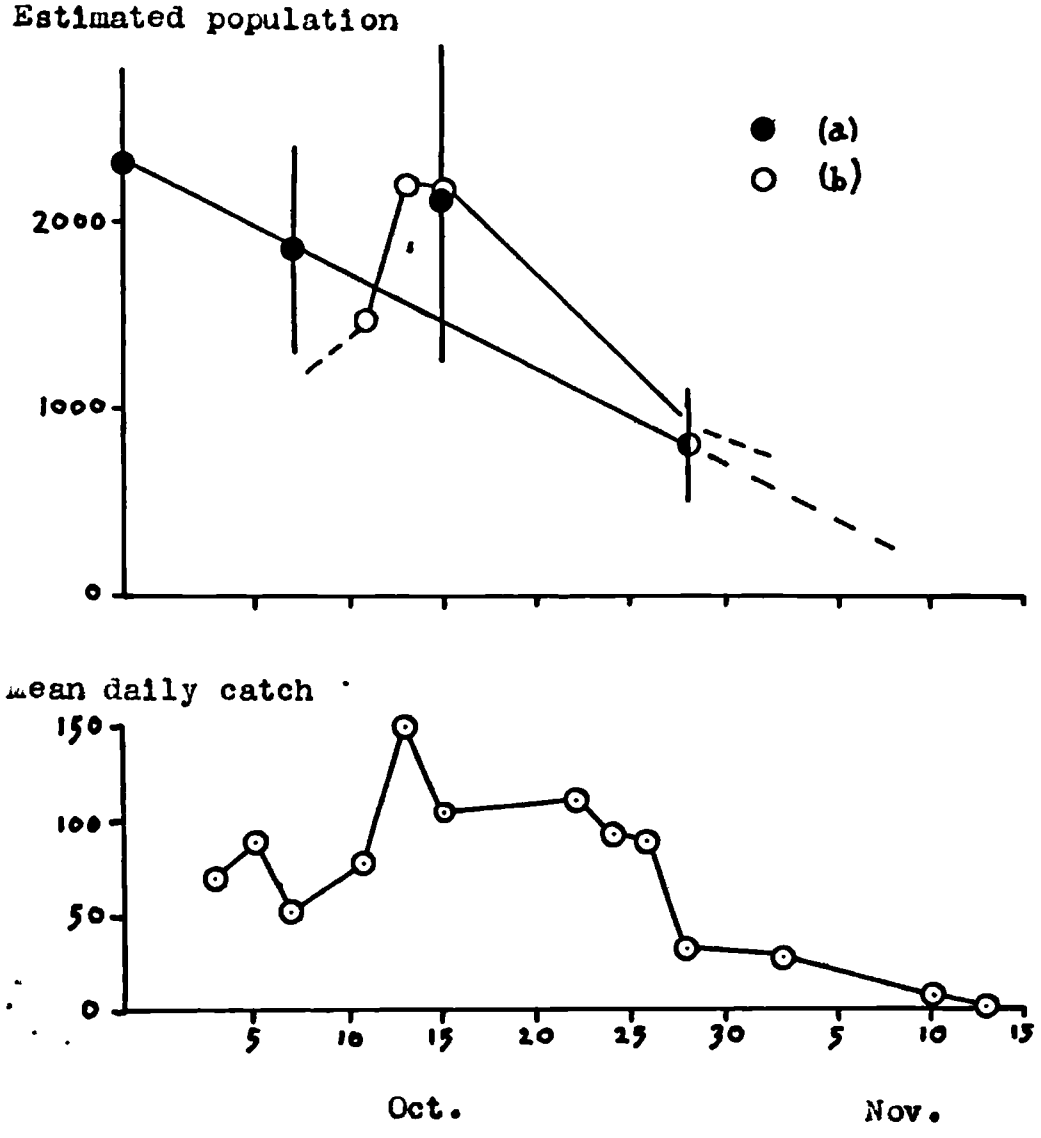


Fig.47(a).

Estimated populations and mean daily catches of N.brevicollis.
Wood Bank plot Autumn 1959.



(Estimated populations (a) with one S.D. on each side)

Fig.47(b).

Estimated populations and mean daily catches of
N.brevicollis
Wood Bank plot Autumn 1960.
(Populations with one S.D. on each side)

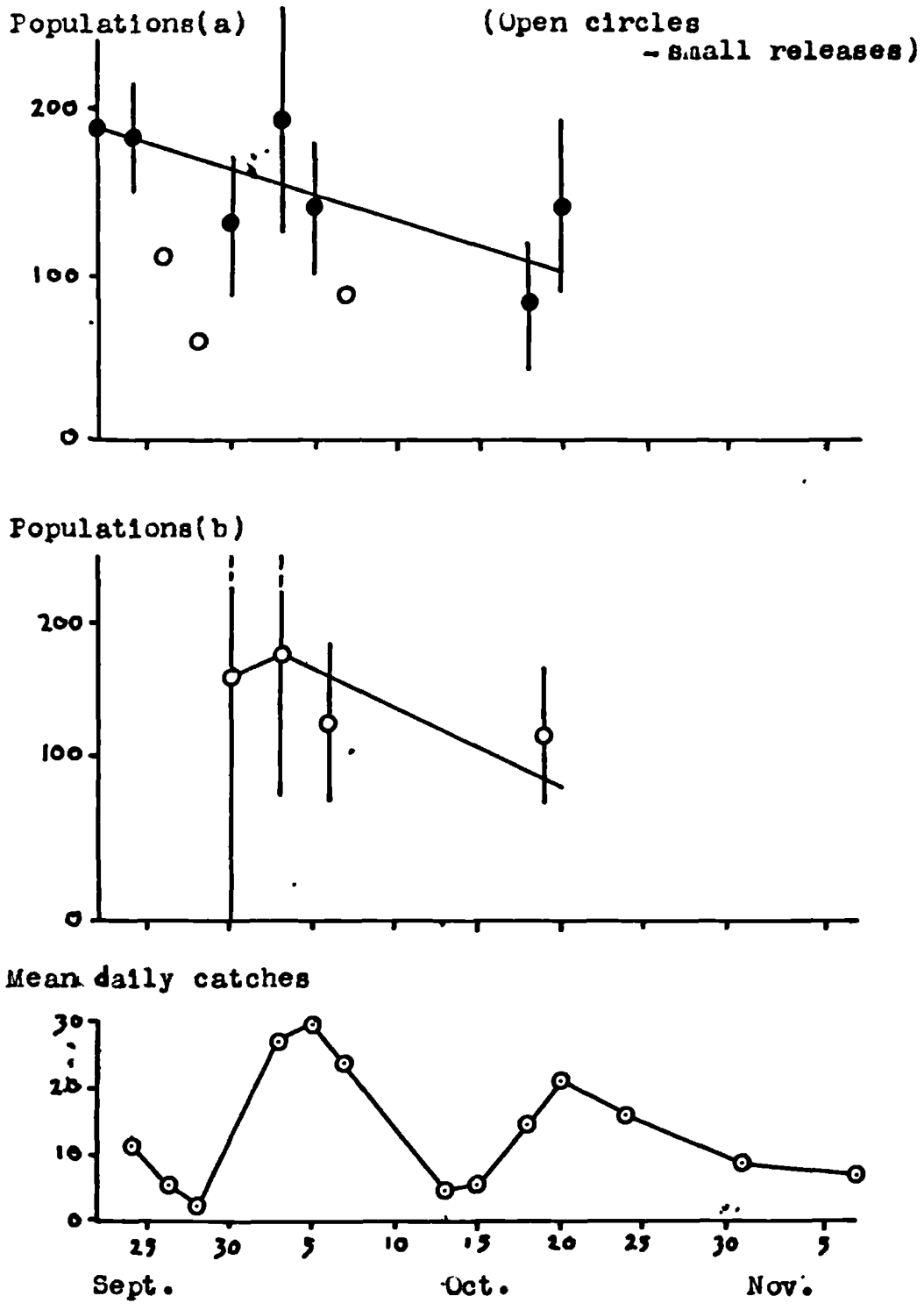


Fig.48.

Weather and activity levels , Wood Bank, Autumn 1959.

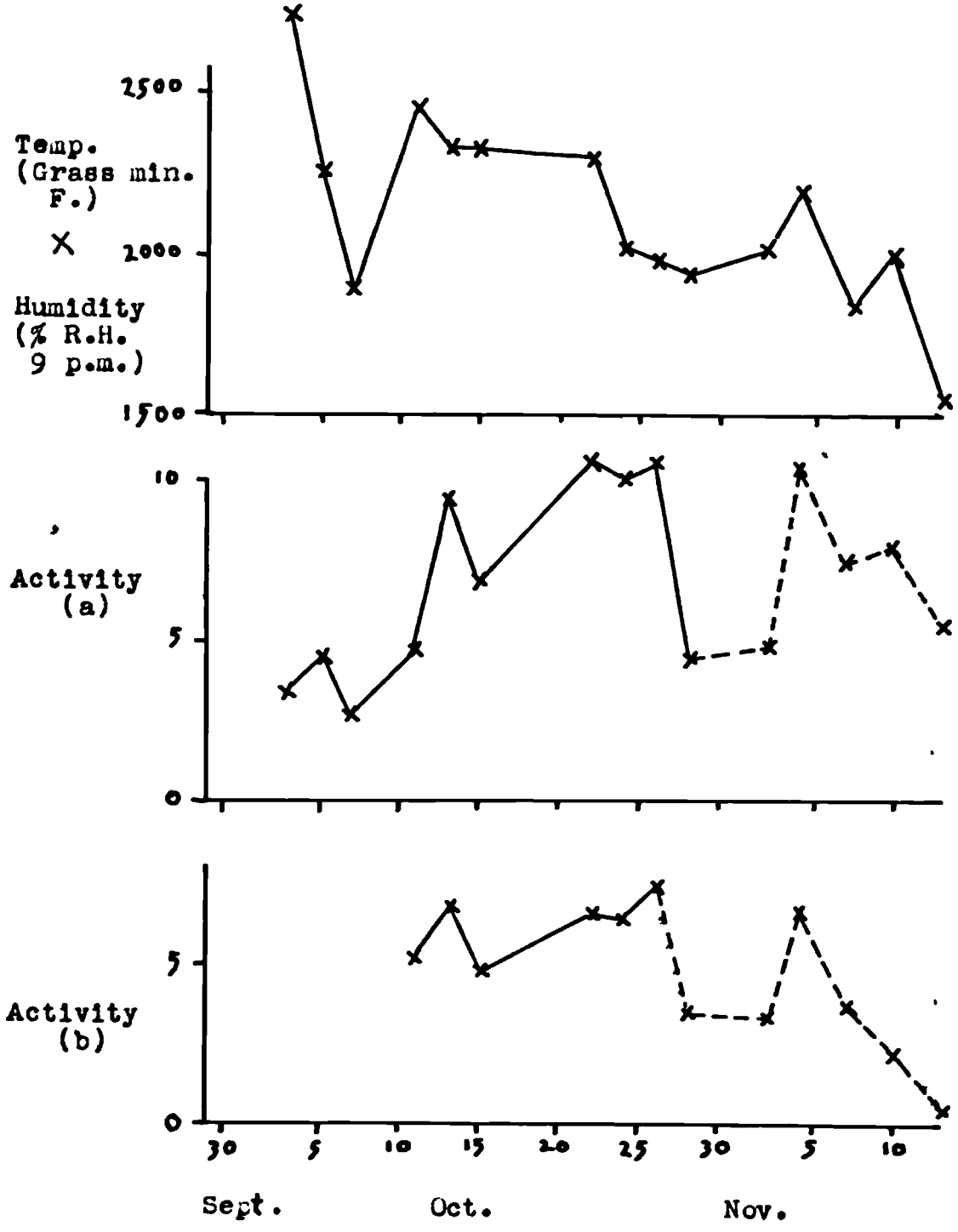


Fig.49.

Estimated populations of N.brevicollis, Wood Bank Autumn 1959.

Recalculated assuming a constant level of activity — o
(2-point running-means plotted)

From recapture data (b) — — — — — - ●

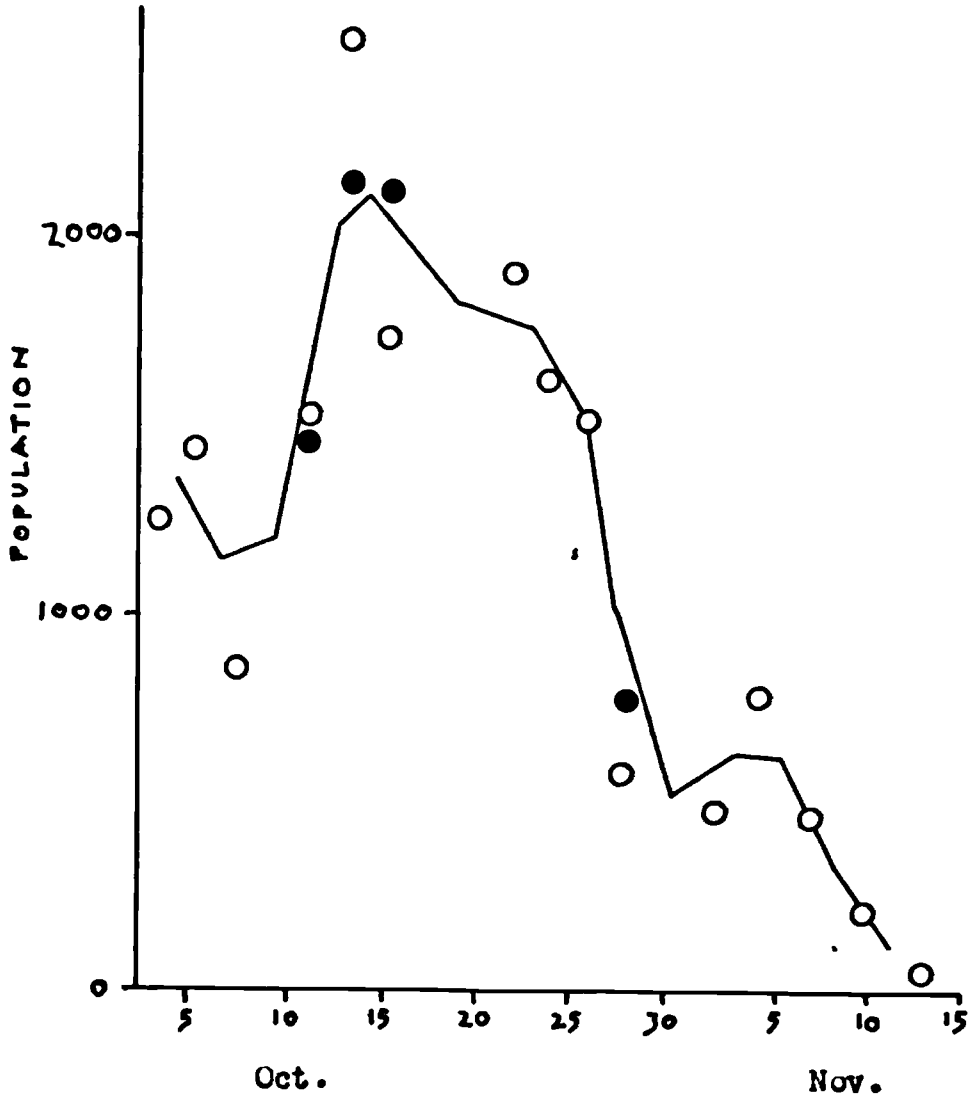


Fig.50.

N.brevicollis mean daily catches and emergence of callows, Wood Bank, March-July 1960.

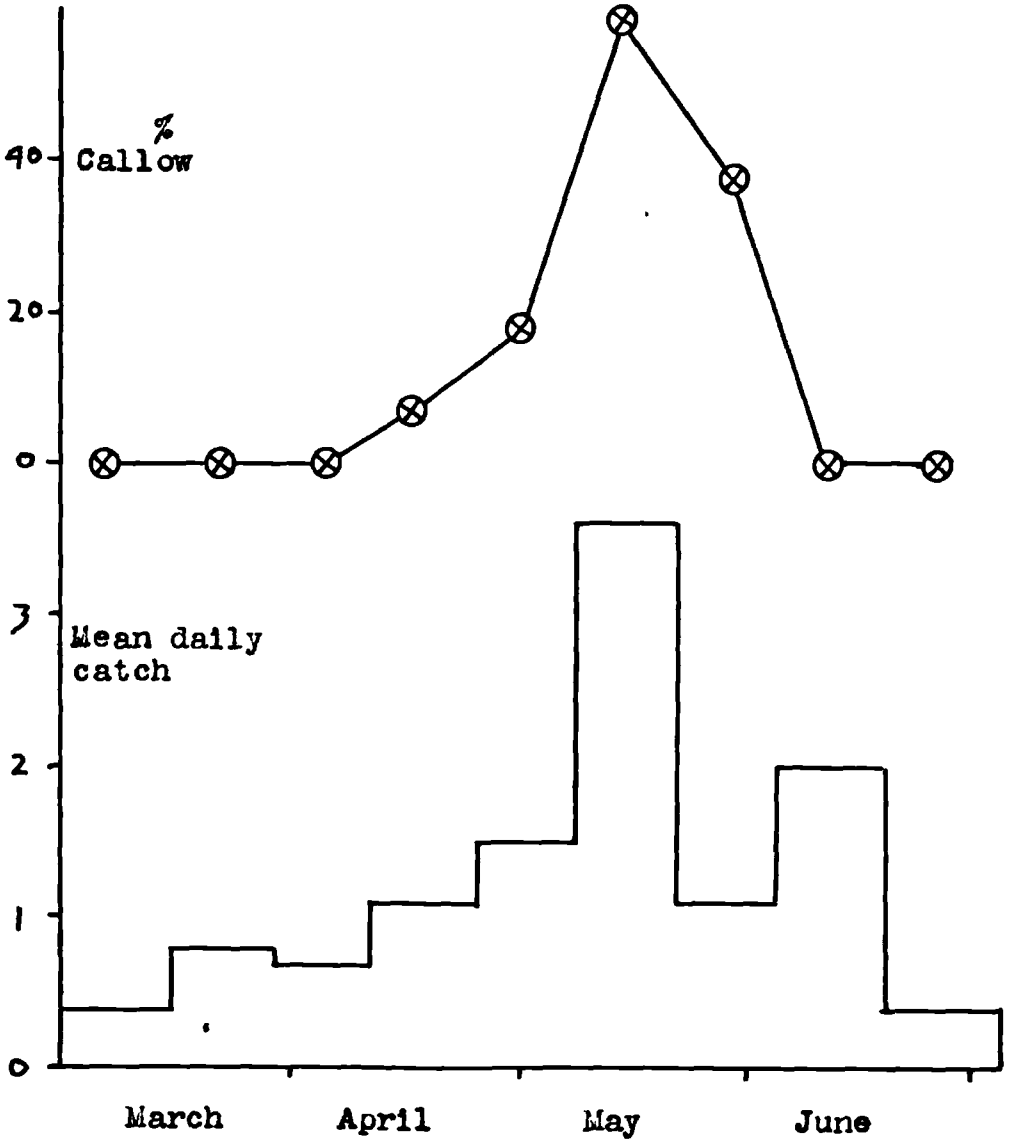
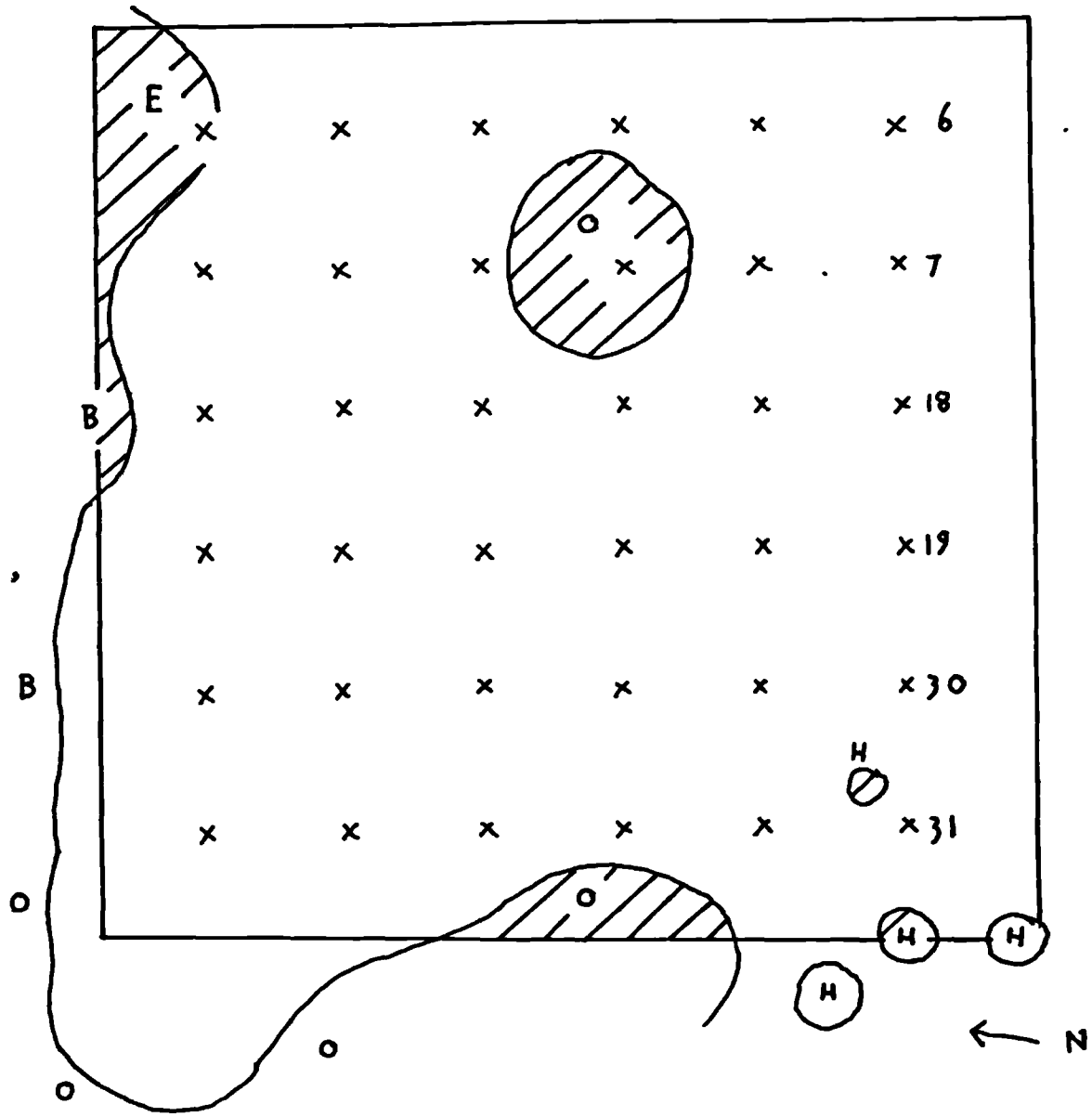


Fig.31.

Vegetation and distribution of traps, Elm Hill heath plot, Summer 1960.



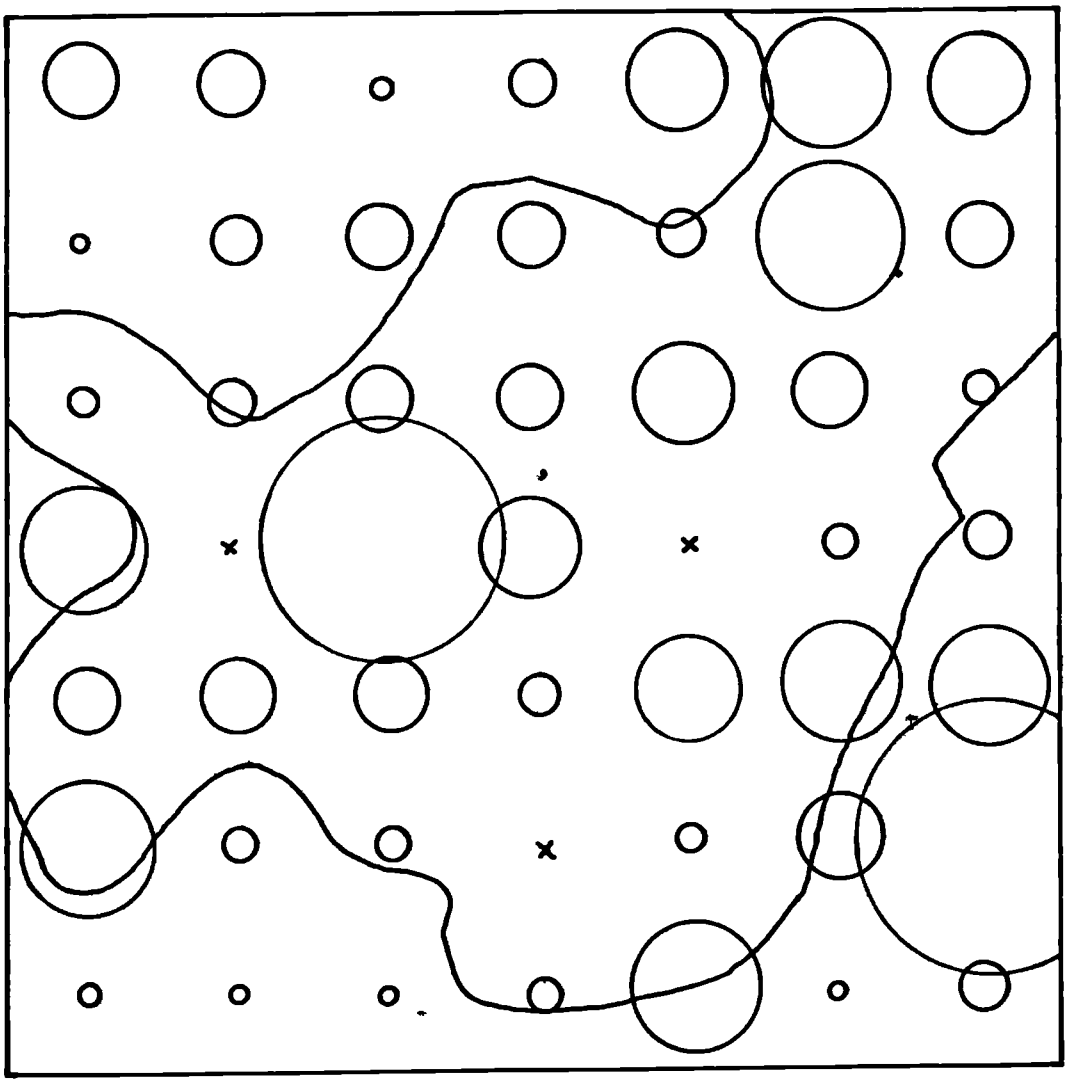
Canopied areas hatched
O Oak
E Elm
B Beech
H Hawthorn

× Trap

10 yds.

Fig.52.

Catches of P.madidus, Wood Bank, 3/5/60-25/II/60.



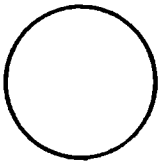
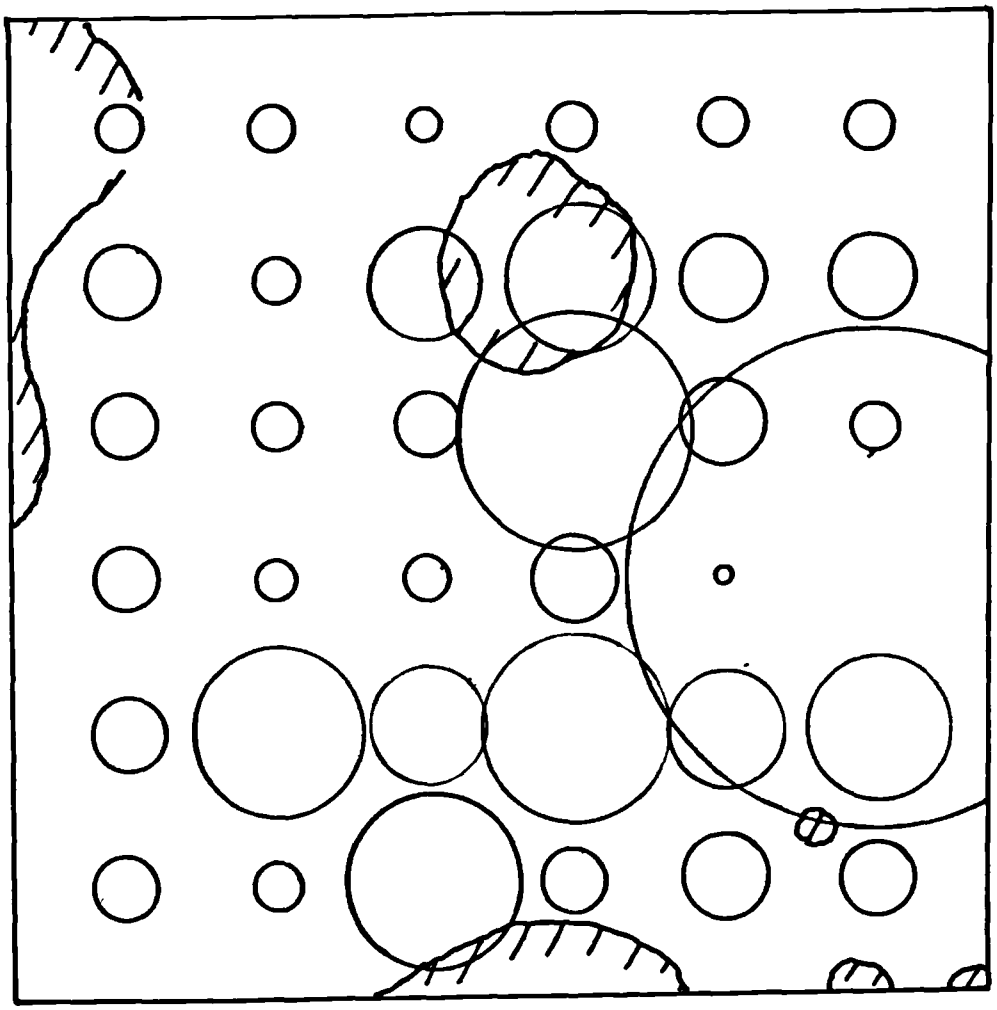
Scale :  10

Fig.53.

Catches of P.madidus, Elm Hill heath, 25/7/60-15/9/ 0.



Scale : ○ 20

Fig.54.

Mean daily catch (36 traps) of P.madidus.
Elm Hill heath plot, June September 1960.
(Continuous line: 2-point running-mean)

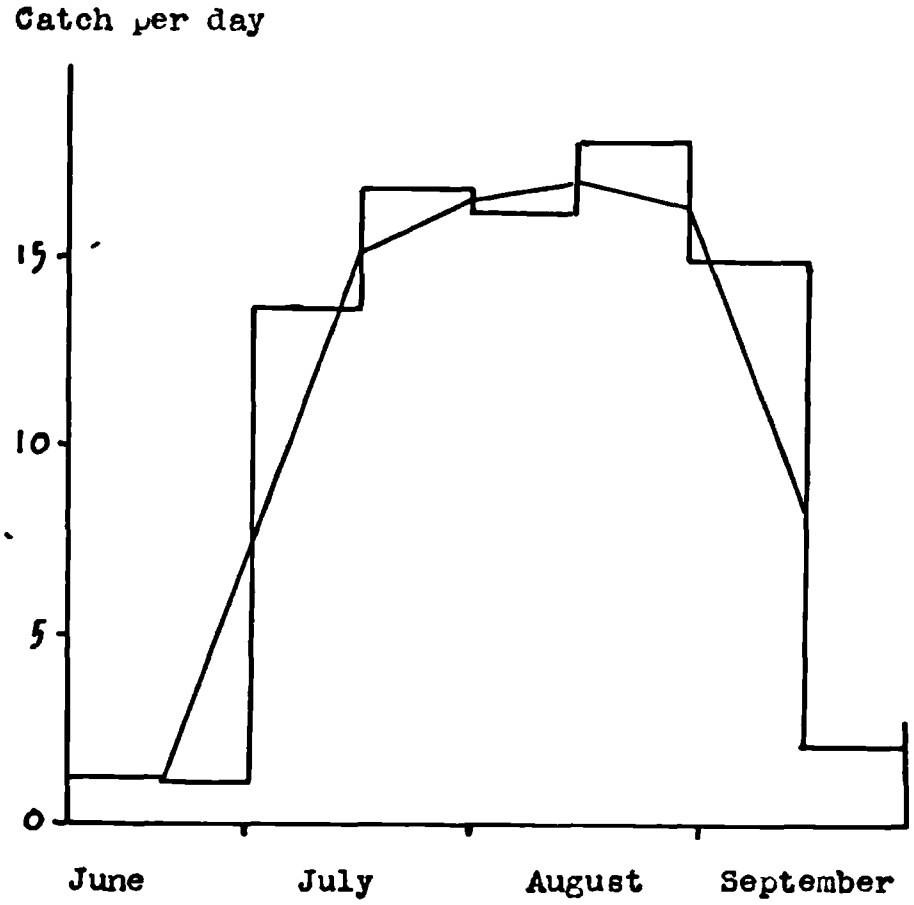
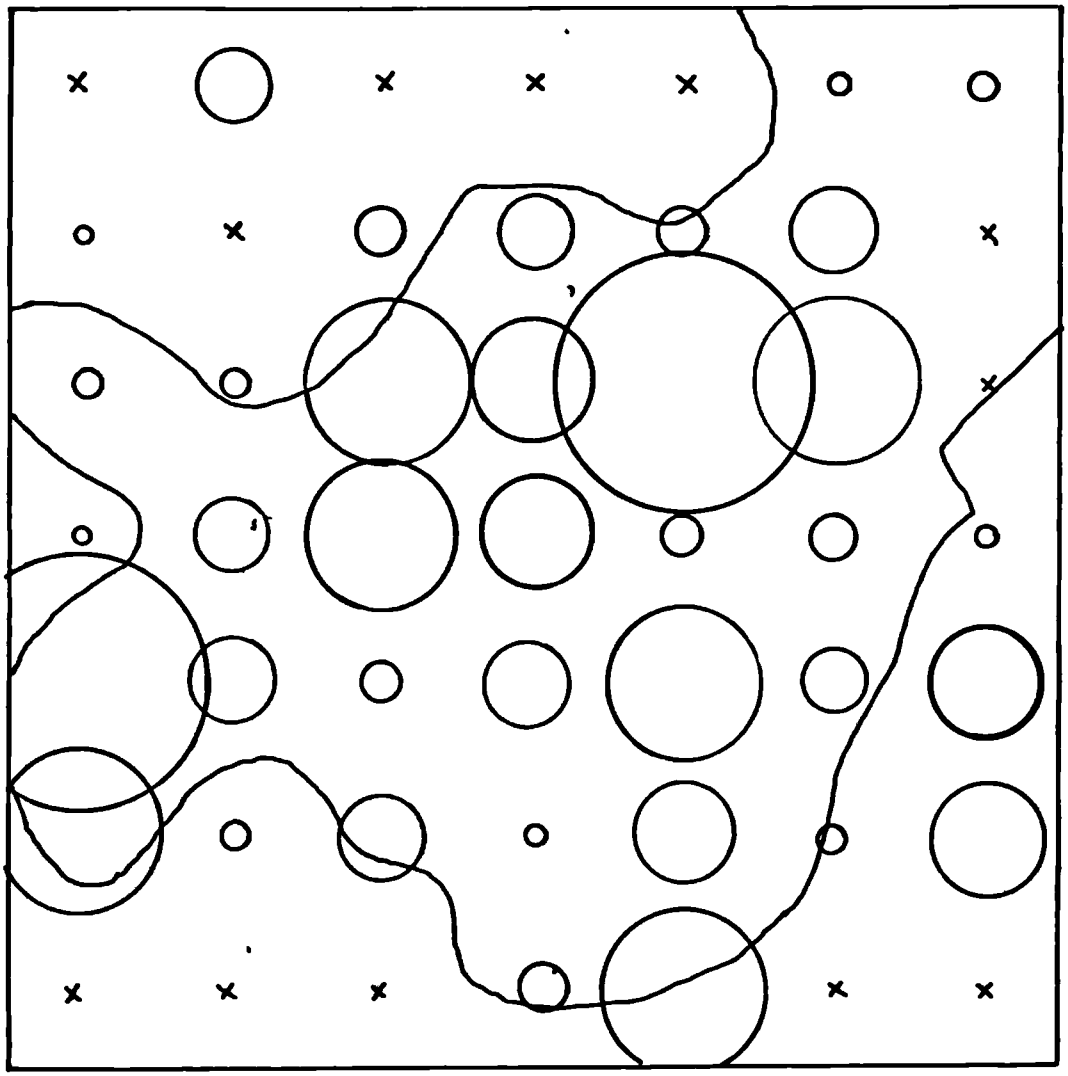


Fig.55.

Catches of Calathus piceus, Wood Bank, Summer 1960.



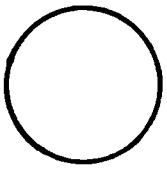
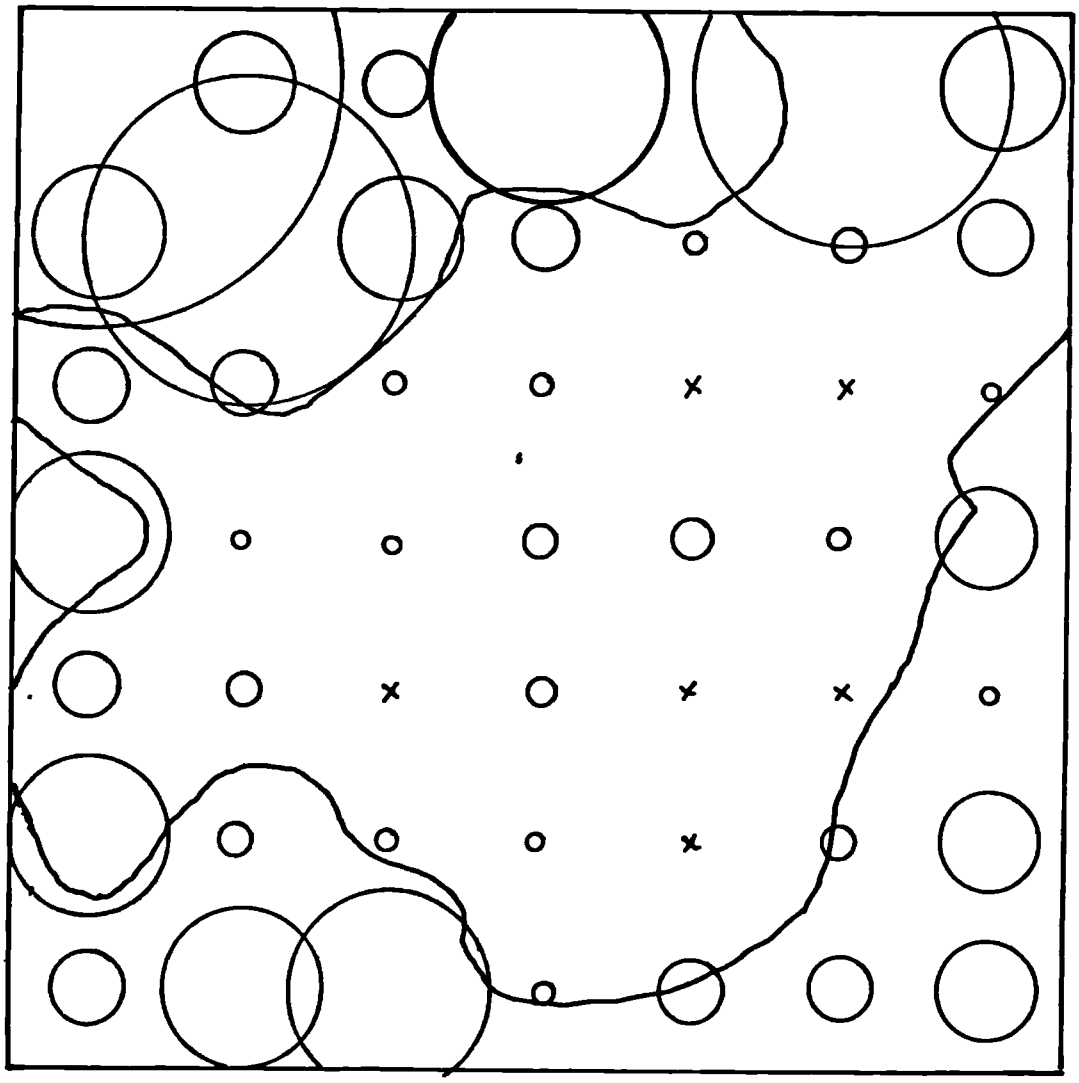
Scale :  10

Fig.56.

Catches of Abax, Wood Bank, Summer 1960.



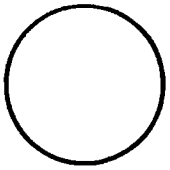
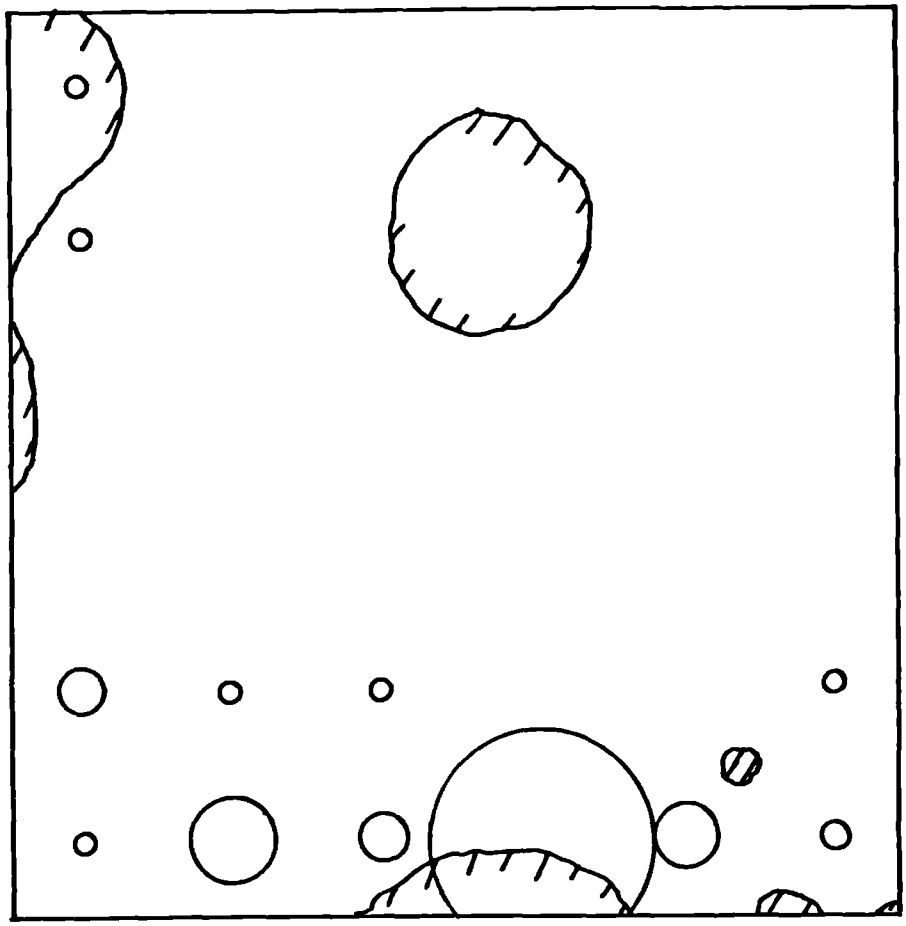
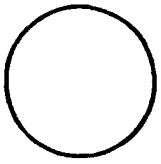
Scale :  10

Fig.57.

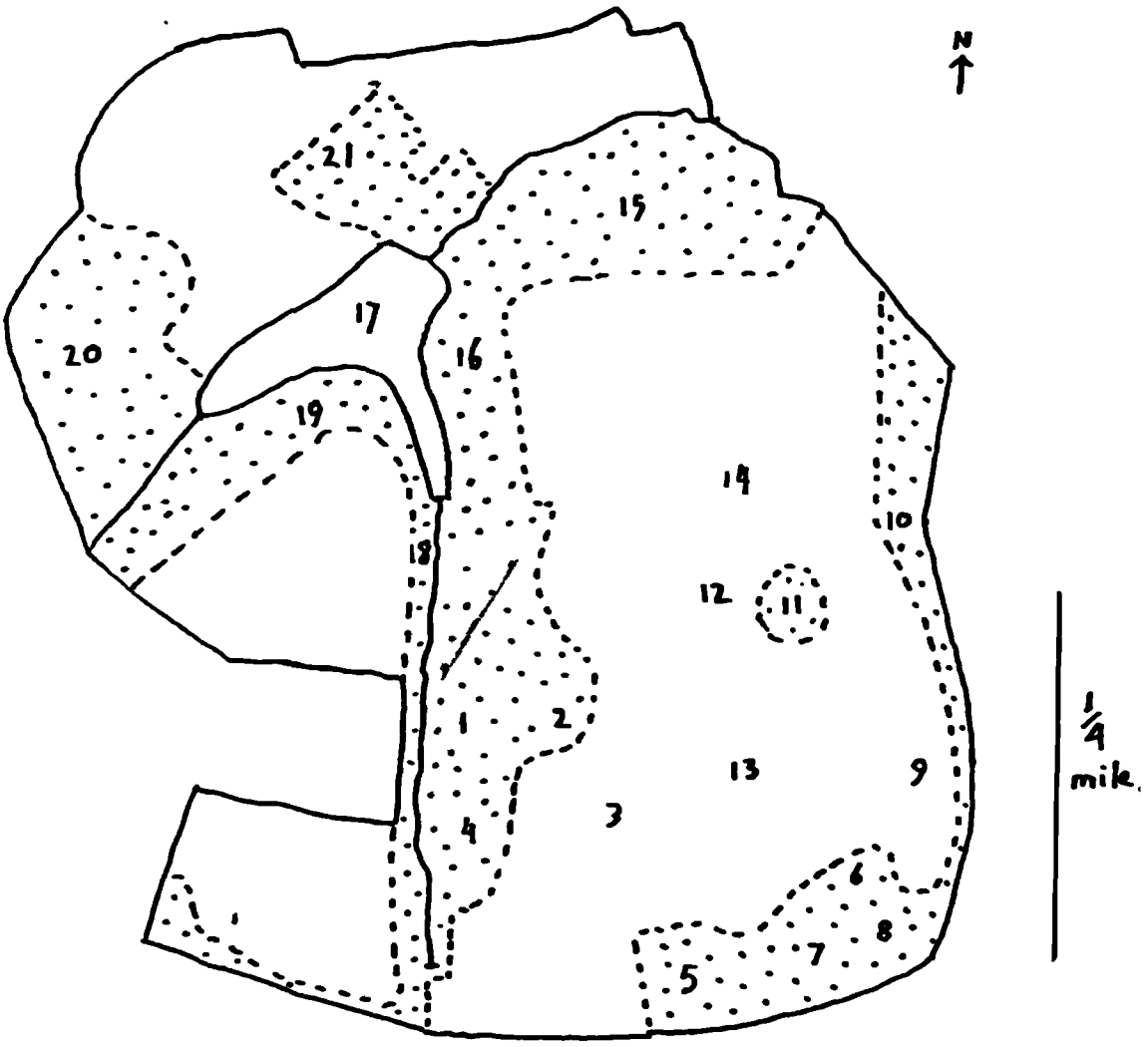
Catches of Abax, Elm Hill heath, 9/7/60 25/8/60.



Scale :  10

APPENDIX

I. Map of Field Station.
(Showing c i f woodland areas (stippled) and localities mentioned i text)



I Wood Bank
2 Elm Hill
3 Drive Hill
4 Rookery Copse
5 South Lodge Wood
6 Garden Wood
7 Heath Wood
8 The Heath
9 N. and S. Gravels
10 Observatory Copse
11 Hill Copse
12 Hill Bottom
13 Silwood Bottom
14 Pond Field
15 Nash's Copse
16 Hell Wood
17 The Lake
18 The Marsh
19 Gunnes thicket
20 Mans Copse
21 Pound Hill

APPENDIX 2. Recorded Carabid agrregations.

The term aggregation is used here to describe an assemblage of individuals in which all, or nearly all, are in physical contact with another individual.

Nebria brevicollis and N. salina. 1954. April. Derbyshire. Derwent Valley. Under stones. The two species occurring separately.

N. brevicollis. 1955. August. Dartmoor. 800'. Above Widecombe. In a clay hedge bank.

Eurynebria complanata L. 1957. July. Devon. Braunton Burrows. Under logs on sand dunes.

Harpalus affinis. 1959. July. Berkshire. Silwood Park. Arable land. Under bricks on bare soil.

Bembidion lampros. 1958. December. Berkshire. Silwood Park. Under bark.

Calathus mollis Mur. 1955. April. Devon. Dawlish Warren. Under logs on sand dunes.

Agonum dorsale. 1954. January.)
A. assimili. 1954. January.) Dorset. Sherborne.
A. mülleri. 1954. November.) Under logs and stones.
A. mülleri also under bark.

Brachinus crepitans L. 1960. April. Dorset. The Fleet. Under stones.

APPENDIX 3. A concentration of Carabidae at Fleet in Dorset April 1960.

On April 20 1960 large numbers of Carabidae were found near Fleet in Dorset, on a South-facing hillside sloping gently down to the lagoon behind the Cheril Bank. The following list of species was made by collecting under and among stones from some two miles of wall of local Jurassic Limestone, between 2.00 and 3.30 p.m. (G.M.T.) in hot sunshine. Numerous isolated stones lying on the ground were investigated, but work was mainly concentrated on 8 points at which walls had collapsed. The walls crossed pasture and plough, and in places were backed by scrub and woodland ; some stones were found in marshy ground near streams and the Fleet lagoon. The underlying rock was Oxford Clay.

It was not possible to make any objective estimate of the relative numbers of different species as individuals were abundant and moved very quickly. The Carabidae found can be divided into four groups:

1) Species abundant everywhere.

Bembidion lampros F.
B. guttula Hbst.
Badister bipustulatus F.
Harpalus affinis Schrank.
H. rufipes Deg.
Acupalpus meridianus L.
Pterostichus cupreus L.
P. strenuus Pz.
Calathus fuscipes Gz.
Agonum dorsale Pont.
Metabletus obscuro-guttatus Drift.
Brachinus crepitans L.

2) Species restricted to damp places:

Bembidion 4-maculatum L.
B. biguttatus F.
B. iricolor Bedel.
Pterostichus nigrita
P. diligens Stm.

3) Species occurring on the edge of woodland or scrub:

Nebria brevicollis F.
Stomis pumicatus Pz.
Abax parallelopipedus Pill. & Mit.

4) Species of which less than 5 individuals were seen:

Leistus fulvibarbis Dej.
Asaphidion flavipes L.
Bembidion properans Steph.
Harpalus dimidiatus Ross.
Amara aenea Deg.
Pterostichus macer Mar.
P. melanarius Ill.

APPENDIX 4. Changes in catch between 1959 and 1960.

Total catches of the 26 species between the beginning of March and the end of September in the 23 traps are compared for the seasons of 1959 and 1960 in table I. In 1960 rather more trapping days were missed than in 1959 but they were generally distributed throughout the period March - September, and in the table the 1960 figures are corrected to the same number of trapping days as 1959.

The table shows a distinct fall in total catches in 1960. In the case of three pairs of species, Harpalus spp., Amara spp., and Calathus fuscipes and C. melanocephalus, the members of each pair possessing very similar life histories, there was no great change in catches. For four species the numbers were not very different in the two years, but they were so small that no definite comparison is possible; they were Carabus nemoralis, N. rufipes, N. substriatus and A. dorsale. Of the rest a single species, Abax, showed higher catches in 1960 than in 1959, while for the remaining 15 species catches fell appreciably. This is shown in the table and is in agreement with the impression gained in the two years from traps of other investigations in a variety of habitats on the Field Station; however, as they were operated in different periods and areas in the two years their catches cannot be conveniently included here. Cychrus and Synuchus, although occurring in the 23 traps in small numbers are included in the species showing an appreciable fall in 1960 as their annual periods of activity were restricted almost completely to July and August, and in the field the difference in numbers in the two years was easily seen.

This general fall in catch may be due to one or more of three factors:

TABLE I. Catches of 26 species in 23 traps - March - September (inclusive) in 1959 and 1960.

Species	1959	1960	1960 corrected to same no.of trapping days as 1959.
Carabus violaceus	73	13	15
C. problematicus	11	1	1
C. nemoralis	4	3	3
Cychrus	7	2	2
Leistus ferrugineus	8	1	1
Nebria brevicollis	817	275	316
Notiophilus rufipes	8	5	6
N. biguttatus	20	10	11
N. substriatus	4	2	2
Loricera	12	2	2
Bembidion lampros	23	4	5
Harpalus rufipes	72	40	46
H. affinis	3	7	8
Amara lunicollis	38	48	55
A. communis	14	8	9
Stomis	22	2	2
Pterostichus caerulescens	30	23	26
P. niger	39	15	17
P. melanarius	32	0	0
P. madidus	1472	416	478
Abax	185	294	338
Calathus fuscipes	18	14	16
C. melanocephalus	9	7	8
C. piceus	189	112	129
Synuchus	7	0	0
Agonum dorsale	3	6	7
Total	3040	1310	
No. of trapping days	215	187	

(a) Disturbance and depletion of Carabid populations following the prolonged trapping which started in the autumn of 1958.

(b) Changes in the effective level of locomotor activity.

(c) Population changes resulting from factors other than trapping.

The effect of trapping is unlikely to be important, for throughout this work virtually all Carabidae occurring in traps were returned to the field and only an essential minimum removed for identification or preservation The main body of traps used in the whole of this work were distributed over an area of half a square mile, and the maximum number in use at any one time rarely rose above 150. If one considers Carabid densities of 26 in 10 square feet of grass heath described in Section A, and the population estimates and mobility discussed later in Section C, the catch of all these traps in half a square mile is negligible.

With respect to (b) above, it was shown in section A that non-simultaneous catches of a species in the same area may not be comparable owing to changes in the level of activity and variation in the extent to which this activity is realised in horizontal movement. It was shown that weather, especially temperature, has a great effect on Carabid activity and catch, and the same climatic factors may also effect growth of vegetation and its resistance to Carabid movement. In terms of weather the summers of 1959 and 1960 showed a distinct contrast. Temperature and rainfall for the two seasons are shown in table II.

During the summer of 1959 clear night skies frequently produced low night temperatures and in the mean values the latter mask the high diurnal temperatures which were recorded. Consequently for the summer months means

of the mean monthly maxima are more significant and are shown in the table. These can be compared, and in conjunction with the rainfall figures show the difference between the hot and dry summer of 1959, and the rather cool, wet one of 1960.

To some extent therefore the low catches of 1960 may be due to a decrease in the level of activity, relative to 1959, induced by low temperatures, but vegetational changes may have contributed also. The general depth and distribution of litter, and the floristic structure of the grass heath were the same in both years, but it was noticeable that in the wet summer of 1960 Holcus mollis, which dominates part of the grass heath, particularly in the vicinity of woodland, showed a growth more vigorous than that of the dry summer of 1959. To some extent this is a shade-tolerant species, and from the account of its biology given by Ovington and Scarfield (1956), it might be implied that, if not responding favourably to an increase in soil moisture, it may benefit from a high humidity. Therefore where H. mollis is an important constituent of the heath its 1960 growth may have impeded Carabid movement and reduced catches. The same may apply to other plant species.

In addition there is the probability that the 1960 fall in catches may be the direct effect of low temperatures. It is noticeable that the only species showing an appreciable increase in 1960 was Abax, which is particularly susceptible to humidity changes. It is a nocturnal species with a distribution centred on shaded woodland habitats, as is shown in Section B, and field observation suggests that activity is stimulated by rain or a high humidity. An attempt was made to demonstrate this by calculating partial correlation coefficients between catch and evening

TABLE II. Mean monthly temperature and rainfall. March 1957 - September 1960.

	March - Sept. 1957.	Oct.1957 - Feb.1958	March - Sept. 1958	Oct.1958 - Feb.1959.	March - Sept. 1959	Oct.1959 - Feb.1960	March - Sept. 1960
Mean Temp. $^{o}F.$	55	43	44	42	56	44	54
Mean Max. Temp. $^{o}F.$	64	48	62	47	67	49	63
Mean Monthly Rainfall (mm.)	46.8	52.1	63.0	49.8	32.3	67.2	47.8

temperature and humidity; catches were low (3-4 per day in the 34 traps visited daily in the summer of 1960) and no significant relation was found. However, Thiele (1960) noticed that the distribution of Abax species within hedges in Germany was determined by humidity. It is possible therefore that a higher rainfall, and hence humidity, in 1960 may be responsible for the increased activity and catch of Abax. This is a humidity effect but conversely high temperatures in 1959 may have stimulated the activity of other species, less dependant upon a high humidity. Therefore weather is probably a factor causing some reduction in catches in 1960, either directly by limiting the level of Carabid activity, or indirectly by its effects on vegetation.

However, there were also indications of changes in absolute numbers. In August 1959 16 sq. ft. of turf on Elm Hill yielded 7 P. madidus, while

in the same period and the same area in 1960 only 4 were obtained from 20 sq. ft.. Estimates were made of the numbers of N. brevicollis in the same area of beech litter in the autumns of both years (Section C), and the maximum population fell from 2,300 in 1959 to 200 in 1960.

It has been argued that in 1959 high temperatures may have stimulated adult activity which was inhibited by low temperatures in 1960, while the susceptibility of Carabid larvae to desiccation would suggest that for them the wet summer of 1960 was more favourable. There is some evidence to confirm the latter statement; it was noticed in the late summer and autumn of 1960 that some species with summer larvae were appearing in large numbers as compared with the same period in 1959, many individuals being callow, for example the September occurrence of P. caerulescens. Other species with similar life histories which were generally more abundant in the autumn of 1960 were N. rufipes, N. biguttatus and Amara lunicollis. If activity was lower in 1960 this must have been a real increase in autumn numbers.

From this it may be inferred that the 1959 weather allowed a high level of adult activity, but acted adversely on larval survival or adult fecundity, hence the small numbers of callows in the autumn of 1959. In 1960 on the other hand adult activity may have been low (probably only a small population surviving from the summer of 1959) combining to give catches lower than in the previous year; 1960 however allowed a successful larval generation, producing relatively large numbers of new adults in the autumn. (Actually these differences in numbers in the two years may be the direct effect of weather on larval and adult survival or fecundity, or reflect indirectly changes in the activity or numbers of parasites, predators or competitors).

One might expect to find differences in the 1959-1960 fall in catch according to type of life history and the relative vulnerability to weather of the stage present in the summer months. The fall in catch in 1960 for the various types of life history are compared in table III. This would appear to show least fall in the summer larvae species, but their large autumn emergence in 1960 has been mentioned. Catches in August and September, that is those occurring after the summer maximum, may be excluded from the comparison of the two years.

Adult overwintering species.	1959	1960
Total catch	156	126
August-Sept. catch	5	35
Thus early summer catch:	151	91

These corrected figures are shown in table III.

The differences in observed fall in catches in 1960 may be compared by the χ^2 test:

1) Fall in catch of summer larvae species compared with that which would be expected if they showed the same % fall as the winter larvae species without diapause.

Summer larvae species (excluding Aug.-Sept. catches)

Observed fall : 60

Expected (50% of 1959 catch) : 75.5.

$$\chi^2_{(1)} = 3.18 \quad P = > 0.05$$

2) Fall in catch of winter larvae species with diapause compared with that which could be expected if they showed the same % fall as winter larvae species without diapause:

TABLE III.

Type of life history	1959	1960 (Corrected)	% fall in 1960
Summer larvae	156	126	19
Summer larvae (excl. Aug.-Sept. catch)	151	91	40
Winter larvae (with summer adult diapause)	836	318	62
Winter larvae (without diapause)	2125	1059	50
Total - Winter larvae	2961	1377	53

Winter larvae species with diapause
- observed fall : 518
Expected (50% of 1959 catch) : 418

$\chi^2_{(1)} = 23.9$ $P = < 0.01$.

This shows no significant difference between the 1960 fall in catches in the summer larvae species and winter larvae species without summer diapause. It also suggests that the fall in catch of the winter larvae species with summer diapause is significantly greater than in those without the summer diapause; but the validity of this difference if applied to all larval overwintering species with the diapause is perhaps doubtful as in numbers a single species, Nebria brevicollis, dominates the group.

It is therefore concluded that these data do not offer any confirmation for the suggestion that type of life history is related to survival during possible unfavourable summer seasons. However in the case of Nebria more evidence is available and this will be considered.

Table IV shows catches of N. brevicollis in 23 traps, of adults in October and November, of larvae between December and March, and the total catch of callows in each year, from autumn 1958 to autumn 1960.

TABLE IV. Catch of Nebria stages 1958 - 60 in 23 traps.

Adults Oct.-Nov. 1958	Larvae Dec. '58 - Nov.'59	Callows 1959	Adults Oct.-Nov. 1959	Larvae Dec. '59 - Mar.'60.	Callows 1960	Adults Oct.-Nov. 1960.
801	97	102	913	68	76	352

The mature adults are more active than the callows or larvae and show a higher catch. Catches of larvae and callows and of adults were lower in 1960 than in 1959 although the mature adults fell proportionately more than the earlier stages. Catches of the two years may be tested for homogeneity if treated as a 3 x 2 Contingency table, χ^2 being calculated by Brandt and Snedecor's formula. (Table V).

TABLE V. Nebria brevicollis - Catch in 23 traps.

Year	Larvae	Callows	Autumn adults	Totals
1958-59	97	102	913	1112
1959-60	68	76	352	496
Totals	165	178	1265	1608
$\chi^2_{(2)} = 25.86$ $P = < 0.001$				

This array shows significant heterogenesty and the 1960 catch of autumn adults is therefore less than a direct relationship with catches of larvae and callows would require. When weather is considered this is to be expected, as that of any autumn is unlikely to bear much relation to that of the preceding spring and winter.

There is however no apparent dependance of autumn catch upon summer weather (table VI). But these autumn adult catches appear to vary with the summer weather of the previous year, that is the season in which their parents reached sexual maturity.

TABLE VI. Catch of Nebria brevicollis stages in 23 traps.

Year	Autumn catch	Summer weather index.* Same year	Previous year
1958	801	391	299
1959	913	216	391
1960	352	301	216

However, if the estimated correlation coefficient ν is calculated between autumn catch and weather index of the summer of the previous year it is found that this relationship is not significant:

$$\nu = 0.935 \quad t = = .82 \quad P = > 0.01.$$

In Canada Edwards (1960) found, empirically, a correlation between grasshopper numbers and the weather, especially temperature, of the preceding three years, but here data were available from a much longer period.

Larval catches would be expected to respond to winter weather but

*Summer weather index = Mean max. temp. (^{o}F) x mean monthly rainfall (mm).

reference to tables II and IV shows no such relation. The three winters between autumn 1958 and spring 1960 were very similar in terms of temperature, and that of 1959-60 which was the most favourable for larvae, being the mildest and wettest (as shown both by table II and by inspection of daily temperature, rainfall and humidity records) was followed by the lowest larval and adult catches.

These three years' observations therefore provide insufficient evidence to confirm or deny a statistically significant correlation between autumn catches of adults and the weather of the periods during which the early stages developed or the previous generation became sexually mature. No explanation can be put forward to account for the difference between the 1960 fall in catch of larval overwintering species with diapause, and the fall in those without. The significance of the adult diapause in N. brevicollis and other species has been discussed in Section B.

Tipton (1960) observed similar fluctuations in numbers of Nebria brevicollis near Reading between 1957 and 1960, which he attributed to weather effects. However, he did not investigate the subject in any detail and the significance of the correlation was not estimated. From the present work it is evident that a statistically significant conclusion requires population estimates and records of pitfall catches from a period of more than three years. The results given here, however, supported by Tipton's observations, do suggest that a profitable long-term study could be made on fluctuations of Carabid numbers in relation to density, distribution of populations and weather.

In support of the suggestion that weather influences the numbers in the following season, it may be recorded that in June 1961, after the wet summer of 1960, collecting at Silwood has shown a number of species, notably *Asaphidion flavipes*, *Harpalus affinis*, *Calathus melanocephalus* and *Agonum dorsale*, to be markedly more abundant.



PL TE 2. Grass heath plot, looking N. to Elm Hill woodland. June 1960.

APPENDIX 6.

TABLES

APPENDIX TABLE I. Total catch of Carabidae in Plot (1) 18/3/59 - 15/5/59 - traps of types A, B and C.

Species / Trap	Pterostichus madidus	P. caerulescens	Amara lunicollis	A. communis	A. aenea	A. familiaris	A. tibialis	Pterostichus vernalis	Bembidion lampros	B. 4-maculatum	Asaphidion flavipes	Trechus 4-striatus	Bradycellus harpalinus	Nebria brevicollis	Total.
1 C			1									1	3		5
2 B	17	3	1	4	1	1			1				1		29
3 A	1		1	1											3
4 B	4		1	1	1								1	1	9
5 C	2		1										2		5
6 A	1														1
7 B	5	2	4	2	1				2	1	1		1		19
8 A	1														1
9 C	3		4	3	1		1	1	1				1		15

APPENDIX TABLE 2. Total catch of Carabidae in Plot (1) 13/7/59 - 29/7/59, traps of types A, B and C.

Trap	Species: Pterostichus madidus	P. melanarius	P. caerulescens	P. cupreus	P. niger	Abax parallelopipedus	Harpalus rufipes	H. latus	Bradycellus harpalinus	Trechus 4-striatus	Calathus fuscipes	C. melanocephalus	C. piceus	Synuchus nivalis	Carabus violaceus	Total
1 C	48	7			1		4	1	1	1	2			2	2	69
2 B	40	1					1	1			1					44
3 A	71	1	1				1				13	3			4	94
4 B	106	2				1	1				5					115
5 C	54	1			2						1	1		1		60
6 A	65	7			3		6	1			8	7	1		1	99
7 B	119	3	1								3	3		2	3	134
8 A	19	4				1					2	4		1	1	32
9 C	34	1			1						2	4		4		46

APPENDIX TABLE 3. Total catch of Carabidae in Plot (2) 18/3/59 - 23/5/59. Traps of types B and C.

Trap	Species	Pterostichus madidus	P. niger	P. strenuus	P. caerulescens	Abax parallelopipedus	Amara communis	Calathus piceus	C. fuscipes	Nebria brevicollis	Loricera pilicornis
1	B	39			1	2		1	1	8	1
2	C	15	1		1	2		2		5	
3	C	12	3		1	3				8	
4	B	8	1	1		1	1		1	5	

APPENDIX TABLE 4. Catch of Carabidae in 9 traps in Hill Bottom (3 white, 3 black, 3 unpainted controls). 4/5/60 - 24/5/60.

Species	Trap 1 B	2 W	3 C	4 W	5 B	6 C	7 W	8 C	9 B
C. campestris		1							
N. brevicollis	1	3		4		6	4	3	1
C. collaris		1		1					
A. flavipes						1			1
B. lampros		3	4	1	2	4	4	11	2
B. bruxellense	2	5	1	1		1		3	
H. affinis		2	1	16	4	4	3	5	1
H. latus									1
H. tardus						1			
H. rufipes					1				2
A. meridianus		1							
A. binotatus				1	1				
A. communis			1				1		
A. lunicollis							1		
A. aenea			1	1	2		2	2	1
A. familiaris				2			2	6	1
P. caerulescens				1	1		3		
P. madidus					1		1		
P. ruficollis			1						
A. mülleri				2	1				
A. dorsale		2							1
	3	18	9	30	13	17	21	30	11

APPENDIX TABLE 5.

Daily fluctuations of catch of 23 permanent traps 13/4/59 - 30/7/59.

Date		Catch	Date		Catch
April	13	14		8	22
	14	12		9	19
	15	10		10	22
	16	3		11	17
	17	10		18	19
	18	3		19	13
	19	5		20	8
	20	1		21	10
	21	2		22	18
	22	8		23	14
	23	4		24	15
	24	13		25	25
	25	8		26	17
	26	4		27	17
	27	18		28	28
	28	3		29	11
	29	3		30	17
	30	15	July	1	9
May	1	4		2	20
	2	10		3	29
	3	9		4	24
	4	8		5	10
	5	5		6	14
	6	4		7	24
	7	9		8	15
	8	28		9	26
	12	58		10	28
	13	31		11	24
	14	25		12	13
	15	29		13	11
	20	13		14	9
	24	19		15	12
	25	15		16	8
	26	3		17	24
	27	4		18	35
	28	15		19	11
	29	7		20	10
	30	22		21	20
	31	19		22	35
June	1	26		23	19
	2	21		24	15
	3	24		25	19
	4	27		26	17
	5	45		27	31
	6	31		28	21
	7	18		29	28
				30	21

APPENDIX TABLE 6. Total catch of Carabidae in South Lodge Wood plots X, Y and Z. 6/5/59 - 6/6/59.

Species / Trap		Notiophilus biguttatus	Nebria brevicollis	Loricera pilicornis	Pterostichus madidus	P. strenuus	Abax parallelopipedus	Stomis pumicatus	Bembidion lampros	Trechus 4-striatus	Calathus piceus
Plot X	1		17								
	2	1	26		2						
	3	1	32		2					1	1
	4		6								4
	5		16	1	6						
	6		23		7						
	7		14		6						2
	8		23		1						1
	9		12		5						
Plot Y	1		18		1						
	2		10		2						
	3	1	25								1
	4		13		2						
	5		11		1						
	6		12								
	7		20								1
	8		9		3		1				
	9		16		2						
Plot Z	1	1	37		3	5					
	2	2	29			1					
	3	1	17								1
	4	3	26								
	5		17		3	1			1		
	6		5		1		1	1			
	7	2	22	1	1						
	8		11			1	1				
	9	2	21		1						

APPENDIX TABLE 7. Sex ratio of P. madidus in 23 traps between 26/4/60 and 23/11/60.
(Periods are defined before Appendix Table 8).

Month	Period	Male catch	Total catch	% male
	5	3	16	18.75
May	6	8	24	33.33
	7	8	21	38.10
June	8	14	28	50.00
	9	33	40	82.50
July	10	50	56	89.28
	11	78	99	78.79
August	12	78	102	76.47
	13	94	117	80.34
	14	36	63	57.14
September	15	5	9	55.56
	16	2	6	33.33
October	17	0	7	0
	18	0	8	0
November	19	0	7	0

APPENDIX TABLES 8 - 15. Catch of common Silwood Carabidae in traps. 1958-1960.

The trapping was divided as far as possible into periods of 14 days. In the following tables for each species the figures on the left indicate the number taken in traps in each period, and those on the right the mean number per day. For all species except *N. brevicollis* and *P. madidus* the latter are X 10, unless shown otherwise.

1958-59.

Period	Dates	Trapping days	Period	Dates	Trapping days
1	Oct. 9 - 21 1958	14	15	May 12 - 25	14
2	" 22 - Nov. 4.	"	16	" 26 - June 8.	"
3	Nov. 5 - 18	"	17	June 9 - 22	"
4	" 19 - Dec. 2	"	18	" 23 - July 6.	"
5	Dec. 3 - 16	"	19	July 7 - 21	"
6	" 17 - Jan.5 1959	21	20	" 22 - 30	8
7	Jan. 6 - 19	14	21	" 31 - Aug. 24	24
8	" 20 - Feb. 3	"	22	Aug.25 - Sept. 8	"
9	Feb. 4 - 17	"	23	Sept.9 - 22	"
10	" 18 - Mar. 3	"	24	" 23 - Oct. 5.	"
11	Mar. 4 - 17	"	25	Oct. 6 - 19	"
12	" 18 - Apr.12	28	26	" 20 - Nov. 3	"
13	Apr.13 - 27		27	Nov. 4 - 20.	"
14	" 28.- May 11				

1960.

Period	Dates	Trapping days	Period	Dates	Trapping days
1	Mar. 1 - 14 1960	10	11	July 17 - 30	13
2	" 15 - 28	5	12	" 31 - Aug. 13	15
3	" 28 - Apr. 11	14	13	Aug. 14 - 27	12
4	Apr. 12 - 25	13	14	" 28 - Sept. 10	19
5	" 26 - May 8	15	15	Sept. 11 - 26	7
6	May 9 - 22	13	16	" 27 - Oct. 10	13
7	" 23 - June 5	16	17	Oct. 11 - 24	13
8	June 6 - 19	12	18	" 25 - Nov. 9	13
9	" 20 - July 2	13	19	Nov. 10 - 23	16
10	July 3 - 16	17			

APPENDIX TABLE 8. Catch in 23 permanent traps. 1958-59.

Period	Species	Mean catch	Daily catch x 10	Species	Mean catch	Daily catch x 10	Species	Mean catch	Daily catch x 10	Species	Mean catch	Daily catch x 10
	N. brevicollis			P. madidus			C. violaceus			C problematicus		
1	272	19.4		25	1.7					2	1.4	
2	288	25.5		41	2.9					1	0.7	
3	191	13.4		15	1.1					.		
4	56	4.0		20	1.4							
5	24	1.7		5	0.4							
6	27	1.3		6	0.3							
7	26	1.8		2	0.1							
8	21	1.5		1	0.1							
9	12	0.8										
10	20	1.4										
11	43	3.1										
12	32	1.1		18	0.6							
13	36	2.6		40	2.9					1	0.7	
14	73	5.2		41	2.9					1	0.7	
15	160	11.4		38	2.7							
16	162	11.6		38	2.7					1	0.7	
17	76	5.4		27	1.9		6	4.3		1	0.7	
18	35	2.5		87	6.2		16	11.3				
19	7	0.5		176	12.5		18	12.9				
20	1	0.1		143	14.3		7	7				
21	6	0.25		770	32.1		22	9.2				
22	25	1.7		62	4.4		3	2.1				
23	64	4.6		26	1.8		1	0.7		5	3.5	
24	97	6.9		6	0.4					2	1.4	
25	433	31.8		18	1.3							
26	395	28.1		16	1.1							
27	96	5.6		6	0.3							

Period	Species	Mean catch	Daily catch x 10	Species	Mean catch	Daily catch x 10
	C. nemoralis			L. ferrugineus		
1				2	1.4	
2				3	2.1	
3	1	0.7		1	0.9	
4				5	3.6	
5				1	0.7	
6						
7						
8						
9						
10	1	0.7				
11	2	1.4				
12						
13						
14	2	1.4				
15						
16				1	0.7	
17				1	0.7	
18				1	0.7	
19				1	0.7	
20						
21						
22						
23				3	2.1	
24				1	0.7	
25						
26						
27						

APPENDIX TABLE 8. (Continued).

Period	Species	Daily catch x 10											
		C. rostroides		N. rufipes		N. biguttatus		N. substriatus		L. pilicornis		B. lampros	
1						2	1.4						
2													
3								1	0.7				
4													
5													
6													
7						1	0.7						
8													
9						1	0.7						
10				2	1.4			1	0.7			1	0.7
11				1	0.7			2.	1.4	1	0.7		
12													
13				1	0.7	3	2.1			4	2.8	2	1.4
14				1	0.7	3	2.1	2	1.4	2	1.4	5	3.5
15				1	0.7	1	0.7			1	0.7	11	7.9
16				2	1.4	9	6.4			2	1.4	4	2.8
17		1	0.7	2	1.4	4	2.8						
18		3	2.1							2	1.4		
19		2	1.4									1	0.7
20		1	1										
21													
22													
23													
24													
25													
26				1	0.7								
27						1	0.6						

APPENDIX 8. (Continued).

Period	Species	Daily catch x 10											
		H. rufipes		H. affinis		A. lunicollis		A. communis		S. pumicatus		P. caerulescens		P. niger	
1												4	2.8		
2												1	0.7	1	0.7
3		1	0.7												
4															
5															
6															
7															
8															
9												1	0.7		
10												2	1.4		
11															
12								1	0.4			1	0.4		
13						1	0.7	3	2.1			6	4.2		
14						1	0.7	1	0.7			4	2.8	1	0.7
15		4	2.9	1	0.7	2	2.1	5	3.5	5	3.5	7	4.9	2	1.4
16		1	0.7			9	6.4	2	1.4	3	2.1	4	2.8	2	1.4
17		5	3.6	2	1.4	12	8.6	2	1.4	4	2.8	2	1.7	2	1.4
18		14	10			6	4.3			5	3.5			5	3.6
19		9	6.4			6	4.3			3	2.1	3	2.1	3	2.1
20		9	9											2	2
21		27	11.25									3	1.25	18	7.5
22		1	0.7											2	1.4
23		2	1.4							1	0.7			2	1.4
24						1	0.7			1	0.7				
25		2	1.4											1	0.7
26															
27															

APPENDIX TABLE 8.(Continued).

Period	Species	Daily catch x 10													
		P. melanarius		A. parallelopipedus		C. fuscipes		C. melanocephalus		C. piceus		S. nivalis		A. dorsale	
1						19	13.6	11	7.9	1	0.7				
2						7	5.0			7	4.9				
3				1	0.7	3	2.1	1	0.7	1	0.7				
4						1	0.7			1	0.7				
5															
6															
7															
8															
9															
10		1	0.7												
11															
12				2	0.7	1	0.4	1	0.4	2	0.7				
13				14	10.0	1	0.7			3	2.1				
14				13	9.3					4	2.9				
15				21	15.0					9	12.9				
16		4	2.8	11	7.9			1	0.7	19	13.6			4	2.8
17		1	0.7	8	5.7					29	20.7				
18		7	4.9	28	20.0			1	0.7	26	18.6				
19		3	2.1	14	10.0					19	13.6	3	2.1		
20		1	1.0	12	12.0	3	3.0	3	3.0	22	22.0	4	4.0		
21		15	6.3	44	18.3	11	4.6	2	0.8	31	12.9				
22				4	2.8	2	1.4			10	7.1				
23				6	4.2			1	0.7	1	0.7				0.7
24		1	0.7	8	5.6					4	2.8				
25				5	3.6	3	2.1			2	1.4				
26				6	4.2										
27								1	0.6						

APPENDIX TABLE 9. Catch in 23 permanent traps. March - November 1960.

	Mean catch		Daily catch x 10									
Period	*P. madidus*		*N. brevicollis*		*A. parallelopipedus*		*C. piceus*		*H. rufipes*		*H. affinis*	
1			22	2.2								
2			11	5.5								
3			5	0.36							2	1.4
4			10	0.77								
5	.10	0.67	13	0.87	10	6.7	1	0.7	2	1.3	1	0.7
6	30	2.31	69	5.31	20	20	11	8.5	1	0.8		
7	29	1.81	40	2.50	14	8.7	19	13.6	2	1.25		
8	17	1.42	60	5.0	23	19.2	15	12.5	12	10.0		
9	32	2.46	4	0.31	23	17.7	5	3.8	4	3.1		
10	37	2.18	3	0.18	37	21.8	10	5.9	3	1.8		
11	69	5.31			55	42.3	12	9.2	4	3.1		
12	73	4.87	2	0.13	58	8.7	15	10.0	9	6.0	2	1.3
13	69	5.75			40	25	14	11.7	1	0.8	4	3.3
14	50	2.63	36	1.89	8	4.2	10	5.3	2	1.0		
15	9	1.28	36	5.14	2	2.9						
16	9	0.69	137	10.54	1	0.8	2	1.4				
17	10	0.77	107	8.23			1	0.8				
18	7	0.5	69	5.31			1	0.8			1	0.8
19	7	0.5	32	2.0								

APPENDIX TABLE 9. (Continued)

	Daily catch x 10											
Period	N. substriatus		N. rufipes		N. biguttatus		C. nemoralis		C. problematicus		C. violaceus	
1												
2												
3												
4												
5					2	1.3						
6	1	0.8	2	1.4	3	2.3					2	1.4
7					3	1.9						
8			2	1.7								
9												
10			1	0.6	2	1.2	2	1.2			5	2.9
11							1	0.8			1	0.8
12	1	0.7									1	0.7
13									1	0.8	3	2.5
14											1	0.5
15												
16												
17												
18												
19			1	0.6								

APPENDIX TABLE 9. (Continued).

	Daily catch x 10											
Period	P. niger		P. caerulescens		P. melanarius		A. lunicollis		A. communis		B. lampros	
1				4								
2												
3			2	1.4								
4												
5			1	0.7			2	1.3			1	0.7
6	1	0.8	1	0.8			1	0.8	2	1.4	2	1.4
7			3	1.9			1	0.6	1	0.6		
8	2	1.7	1	0.8			9	7.5	3	2.5		
9							3	2.3				
10	5	2.9					16	9.4	1	0.6		
11	1	0.8	1	0.8			11	8.5				
12	1	0.7					3	2.0				
13	1	0.8									1	0.8
14	4	2.1	12	6.3			2	1.0	1	0.5		
15			1	1.4								
16			1	0.8							1	0.8
17			2	1.4							1	0.8
18												
19												

APPENDIX 9. (Continued).

	Daily catch x 10											
Period	S. pumicatus		L. ferruqineus		C. fuscipes		C. melanocephalus		C. rostroides		L. pilicornis	
1												
2												
3											1	0.7
4												
5											1	0.7
6	1	0.8	1	0.8								
7												
8	1	0.8										
9												
10												
11					3	2.3	4	3.1				
12					1	0.7			2	1.3		
13					3	2.5	1	0.8				
14					7	3.7	2	1.0				
15					2	2.9					1	1.4
16					1	0.8						
17			3	2.3	2	1.4	1	0.8				
18			1	0.8	2	1.4						
19					2	1.25						

APPENDIX TABLE 10. Daily catches of 11 traps on Elm Hill. May - November 1959.

Period	Species	Daily catch						Daily catch x 10									
		N. brevicollis		P. madidus		C. violaceus		C. problematicus		L. ferrugineus		C. rostroides					
16		10	0.7	11	0.8					1	0.7						
17		15	1.1	2	0.01												
18		27	1.9	75	5.4	9	6.4										
19		12	0.9	79	5.6	1	0.7	3	2.1								
20		1	0.1	63	6.3	4	4										
21		1	0.04	359	14.9	4	1.6	2	0.8			1	0.4				
22		.1	0.07	10	0.7			1	0.7								
23		14	1.0	26	1.8	1	0.7	5	3.5	3	2.1						
24		97	6.9	6	0.4			2	1.4	1	0.7						
25		108	7.9	9	1.3			3	2.1								
26		101	7.2	2	0.14			1	0.7								
27		64	3.8	1	0.06												
		N. biguttatus		L. pilicornis		B. lampros		H. rufipes		A. lunicollis		A. communis					
16		1	0.7			3	2.1			7	4.8						
17		1	0.7			1	0.7			3	2.1						
18		1	0.7			1	0.7	2	1.4	6	4.2	1	0.7				
19		1	1					1	0.7	3	2.1	1	0.7				
20								1	1	1	1						
21				1	0.4			8	3.2	2	0.8						
22																	
23								2	1.4								
24										1	0.7						
25								1	0.7								
26																	
27																	

APPENDIX TABLE 10 (Continued).

	Daily catch x 10											
	S. pumicatus		P. caerulescens		P. niger		P. melanarius		A. parallelepipodus		C. fuscipes	
16	3	2.1							6	4.2		
17			1	0.7					2	1.4		
18			1	0.7	1	0.7	1	0.7	33	23.6	2	1.4
19			1	0.7	4	2.8	5	3.5	7	4.9		
20					5	5			6	6	1	1
21					14	5.8	3	1.3	24	10	3	1.3
22					1	0.7			1	0.7		
23									7	4.9		
24									3	2.1		
25									7	5.0	1	0.7
26									9	6.4	1	0.7
27									5	2.9		

	C. melanocephalus		C. piceus		S. nivalis	
16			15	10.7		
17			8	5.6		
18			93	66.4		
19	1	0.7	78	55.7	3	2.1
20			33	33	3	3
21			52	21.7	1	0.4
22			3	2.1		
23			2	1.4		
24						
25						
26						
27	1	0.6				

APPENDIX TABLE 11. Daily catches of 11 traps on Elm Hill. March - November 1960.

Period	Species	Daily catch						Daily catch x 10									
		N. brevicollis		P. madidus		A. parallelopipedus		C. piceus		A. lunicollis		A. communis		H. affinis		H. rufipes	
1																	
2		1	0.2														
3																	
4		2	0.14														
5		6	0.4	3	0.2	11	7.3	1	0.7	1	0.7						
6		12	0.9	4	0.3	17	13.1	13	10.0			2	1.4	1	0.8		
7		12	0.7	6	0.4	10	6.0	13	8.1							1	0.6
8		9	0.7	11	0.9	16	13.3	20	16.7	3	2.5	1	0.8				
9				8	0.6	8	6.2	10	7.7	1	0.8					3	2.3
10				19	1.1	11	6.5	25	14.7	6	3.5					2	1.2
11				30	2.3	18	13.8	29	22.3	6	4.6					2	1.4
12		2	1.3	31	2.1	8	5.3	24	1.6								
13		1	0.08	48	4.0	3	2.5	37	30.8								
14		8	0.4	13	0.7	4	2.1	4	2.1								
15		49	7.0	3	0.4	2	2.9	3	4.3								
16		78	6	2	0.14			2	1.4								
17		25	1.9	3	0.2			2	1.4								
18		2	0.19	2	0.14												
19		1	0.06	1	0.06												

APPENDIX TABLE 11 (continued)

Period	Species	Daily catch x 10															
		C. problematicus		C. nemoralis		N. biguttatus		N. substriatus		C. fuscipes		P. melanarius		P. niger		P. caerulescens	
1																	
2																	
3																	
4																	
5						2	1.3										
6		1	0.8			2	1.4			1	0.8						
7				1	0.6			1	0.6								
8						1	0.8					1	0.8	3	2.5		
9																	
10		1	0.6			2	1.2										
11																2	1.4
12																	
13				1	0.8												
14																3	1.6
15		2	2.9														
16		4	3.1			1	0.8			1	0.8						
17		2	1.4														
18																	
19																	

APPENDIX 12. Daily catches of two traps in Hill Field. May - September 1959.

Period	Species	Daily catch						Daily catch x 10					
		N. brevicollis		P. madidus		L. pilicornis		B. lampros		H. rufipes		H. affinis	
15		3	0.21	1	0.07			7	4.9	4	2.8	4	2.8
16		3	0.21	6	0.43			13	9.3	8	5.7	7	4.9
17		2	0.14	7	0.5	1	0.7	8	5.7	10	7.1	9	6.3
18				12	0.9			27	19.3	16	11.4	7	4.9
19		1	0.07	11	0.8			7	4.9	8	5.7		
20				9	0.9			10	10	20	20	11	11
21				13	0.5					32	13.4	3	1.25
22		1	0.07					1	0.7	2	1.4		
		A. communis		S. pumicatus		P. caerulescens		P. niger		P. melanarius		C. fuscipes	
15		1	0.7			1	0.7						
16						3	2.1			20	14.3		
17				1	0.7	1	0.7			12	8.6		
18						4	2.8			6	4.3		
19													
20						1	1	1	1	3	3	5	5
21						1	0.4			11	4.6	3	1.25
22						2	1.4					1	0.7

APPENDIX TABLE 13. Daily catches of 3 traps in Hill Bottom April - November 1960

Daily catch x 10

Period	Trapping days	P. madidus		B. lampros		H. rufipes		H. affinis		C. fuscipes		C. melanocephalus		P. melanarius	
5	11			15	14.0	1	0.9	4	3.6					1	0.9
6	14	1	0.7	7	5.0	1	0.7	12	8.8						
		Traps not operated													
10	5	1	2.0	8	16	5	10.0	3	6.0						
		Traps not operated													
12	16	3	1.9	10	6.2	20	12.3	6	3.7	10	6.2				
13	14	1	0.7	4	2.8	21	15	3	2.1	14	10.0	3	2.1	1	0.7
14	17	10	5.9	5	2.9	18	10.6	3	1.8	17	10.0			12	7.1
15	17			2	1.2	1	0.6	1	0.6	2	1.2	1	0.6	1	0.6
16	7			2	2.9					4	5.7	2	2.9	2	2.9
17	12	1	0.8	3	2.5	1	0.8					2	1.7		
18	13			2	1.4							1	0.8		
19	16			2	1.25							1	0.6		

Period	Trapping days	P. caerulescens		N. substriatus		A. dorsale		C. violaceus		C. nemoralis		L. pilicornis	
5	11	1	0.9	1	0.9	2	1.6						
6	14	5	3.5	63	2.1								
		Traps not operated											
10	5												
12	16							1	0.6				
13	14	3	2.1									2	1.4
14	17	4	2.4					1	0.6				
15	17	1	0.6										
16	7												
17	12	3	2.5	2	1.7					1	0.8		
18	13			2	1.4					1	0.8		
19	16												

APPENDIX TABLE 14. Daily catches of 49 traps on Wood Bank. April - November 1960.

		Daily catch						Daily catch X 10									
Period	Trapping days	N. brevicollis		A. parallelopipedus		C. piceus		P. madidus		C. problematicus		N. biguttatus		N. rufipes	
4	5	4	0.8	1	0.2	1	0.2								
5	10	10	1	9	0.1	1	0.1	1	0.1			2	2.0	2	2.0
6	13	29	2.23	51	2.15	28	2.15	11	0.85			10	7.7		
7	8	9	1.125	22	2.75	20	2.5	8	1.0			3	0.4		
8	13	15	1.15	33	2.54	13	1.0	9	0.69			8	6.2	4	3.1
9	15	3	0.20	16	1.07	30	2.0	32	2.13			4	3.1	3	2.0
10	16	1	0.625	43	2.69	31	1.94	36	2.25	2	1.2	4	2.5	1	0.6
11	13	1	0.08	48	3.69	50	3.85	68	5.23			1	0.8	1	0.8
12	14			34	2.43	28	2.0	41	2.93	1	0.7				
13	13	1	0.08	39	3.0	78	6.0	44	3.34	1	0.8			1	0.8
14	15	20	1.33	8	0.53	18	1.38	9	0.6	1	0.7	1	0.7		
15	5	64	12.8	5	1.0	3	0.6			3	6.0	2	0.4		
16	12	196	18.33	6	0.5	5	0.42	3	0.25	1	0.8	1	0.8		
17	17	124	7.29	1	0.06	1	0.06	1	0.06	2	1.2	3	1.8		
18	13	80	6.1									1	0.8	1	0.8
19	5	9	1.8					1	0.06					3	1.8

Period	Trapping days	P. niger		L. ferrugineus		P. melanarius		L. pilicornis		S. pumicatus		C. rostroides	
4	5												
5	10												
6	13	1	0.8							1	0.8		
7	8	1	0.1							1	1.2		
8	13									1	0.8		
9	15												
10	16	2	1.2					1	0.6				
11	13	1	0.8			1	0.8						
12	14	1	0.7										
13	13	1	0.8									2	1.6
14	15			4	3.1							2	1.5
15	5												
16	12												
17	17												
18	13												
19	5	1	0.6										

APPENDIX TABLE 15. Daily catches of 24-36 traps on Elm Hill. (In period 10 traps were increased from 24 to 36 and catches are expressed as 100 x catch per trap-day).

Species Period	Trapping days	P. caerulescens		P. madidus		A. lunicollis		A. communis		N. brevicollis		H. rufipes		A. parallelopipidus	
7	168	8	4.76	6	3.57	1	0.60	2	1.19	5	2.98	1	0.60		
8	242	8	3.31	12	4.96	13	5.37	7	2.89	9	3.72				
9	242	8	3.31	12	4.96	34	14.05	5	2.07			5	2.07	2	0.83
10	600	3	0.50	112	18.67	89	14.83	5	0.83	1	0.17	7	1.17	20	3.33
11	468	1	0.21	217	46.4	69	14.74			1	0.15	24	5.13	13	2.78
12	352	1	0.28	183	52.0	15	4.26					12	3.41	5	1.42
13	504	1	0.20	248	49.2	1	0.20			2	0.40	3	0.60	3	0.60
14	684	144	21.05	351	51.3	1	0.15	1	0.15	10	1.5	2	0.29	6	0.88
15	54	5	9.26	20	18.5	1	1.85			7	12.96				

		C. violaceus		C. nemoralis		C. fuscipes		C. melanocephalus		P. niger	
7	168										
8	242										
9	242										
10	600	3	0.50			1	0.17	3	0.50	3	0.50
11	468	6	1.28	2	0.43	4	0.85	1	0.15	1	0.15
12	352	3	0.85			7	1.99	4	1.14		
13	504	2	0.40			7	1.4	2	0.40	2	0.40
14	684			1	0.15	23	3.36	4	0.58	11	1.61
15	54	1	1.85			1	1.85	1	1.85		

APPENDIX TABLE 16. Carabidae occurring in 13 traps of Transect 1. 13/5/59 - 24/7/59.

Species \ Trap	1	2	3	4	5	6	7	8	9	10	11	12	13
Abax parallelopipedus								1		2	3	1	2
Carabus problematicus	1												1
Calathus piceus	1										1	9	2
Notiophilus rufipes												1	1
Nebria brevicollis	16	2	1	1	1		5		3	8	2	4	2
Pterostichus niger	2		2	2									3
P. melanarius					1								
P. madidus	6	11	3	6	2	6	2	9		20	24	15	7
Carabus nemoralis	1	1	1										
Calathus rufipes		2											1
Amara communis			3	2	2	5	1	2	2	2			
A. lunicollis	1	9	6	5	7	12	8	8	3	1	2		
Pterostichus caerulescens			2		2		3			1			
Bembidion lampros	1	3	3	5	3	2	3						
Harpalus rufipes					1	3	1	2					
Carabus violaceus			1	1	2	1				1	2	1	
Synchus nivalis							1			1			

APPENDIX TABLE 17. Carabidae occurring in 11 traps of transect 2) 27/5/59-25/11/59 and 2/3/60-30/11/60.

Species	Trap 1	2	3	4	5	6	7	8	9	10	11
N. brevicollis	56	167	125	74	33	18	6	13	2	30	69
C. piceus	29	104	121	94	69	89	35			2	1
N. biguttatus		6	2	2		3					
A. parallelopipedus	32	12	12	31	24	30	20	14	6	13	13
C. problematicus	1	1	4	4	6	3	4	2			
L. ferrugineus					1			3			
S. pumicatus	1	1									
P. niger	2		2	3	7	6	4	2	1		
P. madidus	32	64	59	98	50	95	83	121	108	151	66
C. violaceus	3			4	1	10		4	1	1	2
S. nivalis					2	1	4				
P. melanarius	1	1		1	3				1		4
A. communis										5	1
A. lunicollis								1	4	16	16
C. fuscipes			1				1	2	1	2	3
P. caerulescens								4	1	8	4
H. rufipes								4	3	8	5
B. lampros								1	1	3	2

APPENDIX TABLES 18-30. Daily activity of Carabid species.

Table 18. Autumn 1958. Pterostichus madidus: 2 jars of 6
P. niger 2 jars of 5
73 visits.

Time (G.M.T.)	% Activity P. madidus	P. niger
6 a.m.		
7		
8		
9		
10		
11		
12 noon		
1 p.m.		
2	1.7	
3	6.25	
4	4.2	
5	5.2	
6	16.7	13.3
7	15.0	18.0
8	7.3	48.8
9	6.2	25.0
10	8.3	45.0
11	4.2	27.5
12 m'night	2.1	25.0
1 a.m.		45.0
2	4.2	15.0
3		30.0
4		15.0
5		
6		

S.R. 6.30 a.m. G.M.T.
S.S 5.00 p.m. "

APPENDIX TABLE 19. Spring 1959.

Nebria brevicollis: 2 jars of 10

Abax: 2 jars of 5

Carabus problematicus: 2 individuals

95 visits.

Time (B.S.T.)	% activity Nebria brevicollis	Abax parallelopipedus	Carabus problematicus
6 a.m.			
7			
8			
9			
10			
11			
12 noon			
1 p.m.			
2			
3			
4			
5		2.5	
6			
7	1.25	10.0	
8		6.0	
9	25	54.0	37.5
10	33.7	42.5	37.5
11	34.0	52.9	62.5
12 m'night	33.7	55.0	83.3
1 a.m.	32.5	37.5	50.0
2	16.7	13.3	25.0
3	10	6.7	50.0
4	6.7	10.0	
5	3.3		
6			

SR 5.30 a.m. B.S.T.

SS 8.30 p.m. "

APPENDIX TABLE 20. Spring 1959 (Continued).

N. substriatus: 1 jar of 5.

N. biguttatus: 2 jars of 5.

A. ruficorne: 1 jar of 5.

Time (B.S.T.)	% Activity		
	Notiophilus biguttatus	N. substriatus	Agonum ruficorne
6 a.m.			
7			
8			
9	8.5	13.3	
10	7.5	10.0	
11	10	20.0	
12 noon	15.1	50.0	
1 p.m.	40.0	30.0	
2	24.7	20.0	
3	40.0	30.0	
4	20.0	20.0	
5	31.5	40.0	
6	15.0	20.0	
7	5.7	60.0	
8	4.0	5.0	
9			30.0
10		10.0	60.0
11			50.1
12 m'night			50.0
1 a.m.			35.0
2			46.7
3			33.3
4			20.0
5			
6			

APPENDIX TABLE 21. Spring 1959 (Continued)

Loricera: 1 jar of 5.

B. lampros: 3 jars of 10.

Asaphidion: 1 jar of 5.

Time (B.S.T.)	% activity		
	Loricera pilicornis	Bembidion lampros	Asaphidion flavipes
6 a.m.			
7		1.1	
8			
9		2.5	10.0
10	4.0	14.0	10.0
11	4.0	20.0	28.0
12 noon	12.0	20.1	48.0
1 p.m.	32.0	20.7	60.0
2	10.0	24.2	50.0
3	5.0	32.5	55.0
4	5.0	25.8	45.0
5	5.0	35.0	50.0
6	13.3	13.3	46.7
7	10.0	25.8	30.0
8	4.0	4.7	15.0
9	16.0	6.0	8.0
10	14.0	5.0	13.0
11		1.4	
12 m'night		0.8	
1 a.m.		1.7	
2			
3			
4			
5			
6			

APPENDIX TABLE 22. Spring 1959 (Continued).

P. caerulescens: 1 jar of 5.

P. madidus: 3 jars of 5.

P. niger: 3 jars of 5.

Time (B.S.T.)	% activity		
	P. caerulescens	*P. madidus*	*P. niger*
6 a.m.			
7			
8			
9			
10			
11	15.0	2.6	
12 noon	20.0	4.0	
1 p.m.	28.0	4.0	
2	40.0	1.7	
3	35.0	1.7	
4	40.0	3.4	
5	30.0	3.4	
6	33.3	13.4	2.2
7	15.0	16.7	1.7
8	8.0	13.4	
9		12.0	10.7
10	10.0	10.0	26.7
11	2.9	5.8	18.7
12 m'night	5.0	11.6	53.3
1 a.m.	5.0	10.0	33.3
2	6.7	2.2	4.4
3		2.2	2.2
4			2.2
5			
6			

APPENDIX TABLE 23. Spring 1959 (Continued).

A. assimile: 5

A. dorsale: 5

Cychrus: 3

Time (B.S.T.)	% Activity Agonum assimile	A. dorsale	Cychrus rostroides
6 a.m.			
7			
8			
9			
10			
11			
12 noon			
1 p.m.			
2			
3			
4			
5			
6			
7			
8			
9	48.0	40.0	
10	55.0	50.0	6.7
11	40.0	86.7	14.3
12 m'night	60.0	90.0	33.3
1 a.m.	20.0	46.7	25.0
2	13.3	33.3	
3		40.0	
4		30.0	
5		50	
6			

APPENDIX TABLE 24. Summer 1959.

Pterostichus niger: 1 jar of 5.
P. melanarius: 1 jar of 10
Abax parallelopipedus: 1 jar of 5.
72 visits.

Time (B.S.T.)	% activity *P. niger*	*P. melanarius*	*Abax*
6 a.m.			
7			
8			
9			
10			5.0
11			
12 noc.			
1 p.m.			
2			
3			
4			
5			
6			6.7
7			
8			
9	6.7		22.2
10	60.0	13.3	66.7
11	46.7	23.3	60.0
12 m'night	45.0	25.0	50.0
1 a.m.	35.4	20.0	40.0
2	20.0		60.0
3	20.0	10.0	60.0
4	40.0		20.0
5			
6			

SR 5.15 a.m. B.S.T.
SS 8.45 p.m. "

APPENDIX TABLE 25. Summer 1959 (Continued).

Pterostichus madidus: 2 jars of 5
2 jars of 10
2 jars of 25

Time (B.S.T.)	% activity *P. madidus* 10 (5 per jar)	*P. madidus* 20 (10 per jar)	*P. madidus* 50 (25 per jar)
6 a.m.			
7			
8			2.0
9	3.3		0.7
10			0.5
11	2.5	2.0	0.4
12 noon	4.0		2.0
1 p.m.	16.7		2.0
2	3.3		1.3
3	4.0	1.0	1.6
4	2.5	1.2	1.0
5	2.5	1.0	0.8
6	10.0		1.3
7	7.5	1.2	2.0
8	7.5	3.2	
9	20.0	6.7	3.3
10	40.0	16.7	9.3
11	16.7	11.7	8.7
12 m'night	17.5	5.0	12.0
1 a.m.	10.0	8.3	6.7
2	35.0	2.5	13.0
3	30.0	25.0	10.0
4	20.0	5.0	2.0
5		5.0	8.0
6			

APPENDIX TABLE 26. Summer 1959 (Continued).

Calathus piceus: 1 jar of 10.

Harpalus rufipes: 1 jar of 15.

Amara lunicollis: 1 jar of 10.

Time (B.S.T.)	% activity *C. piceus*	*H. rufipes*	*A. lunicollis*
6 a.m.			
7			
8			
9			
10		3.3	7.5
11		2.7	2.0
12 noon			8.0
1 p.m.			15.0
2			13.0
3			16.0
4			30.0
5		2.7	22.0
6			16.7
7		8.3	16.7
8		10.0	10.0
9		24.5	20.0
10	55.0	53.3	36.7
11	36.7	72.5	25.0
12 m'night	32.5	65.0	25.0
1 a.m.	36.7	46.7	20.0
2	20.0	60.0	10.0
3	20.0	33.3	20.0
4	10.0	60.0	20.0
5		20.0	
6			

APPENDIX TABLE 27. June-July 1960.

C. nemoralis: 1 individual.
N. rufipes: 1 jar of 5.
H. affinis: 2 individuals.
S. pumicatus: 2 individuals.
126 visits.

Time (B.S.T.)	% activity			
	C. nemoralis	N. rufipes	H. affinis	S. pumicatus
6 a.m.				
7				
8		18.0	~~20.0~~	
9		83.3	~~83.3~~	
10		75.0	~~33.3~~	
11		100.0	~~57.1~~	
12 noon		72.6	~~75.0~~	
1 p.m.		55.5		
2		78.6		
3		64.7		
4		70.0		
5		80.0		
6		48.1		
7		61.7	14.75	
8	12.5	48.1	20.0	
9	12.5	24.1	20.0	
10	25.5	38.1	29.5	
11	75.5	7.7	42	18.0
12 m'night	77.8	13.2	50	82.0
1 a.m.	80.0	21.2	62 ~~82.67~~	41.7
2	83.3		62 ~~100.0~~	42.8
3	75.0		~~100.0~~	25.0
4				50.0
5				
6			~~12.5~~	

APPENDIX TABLE 28. June-July 1960 (Continued).

A. communis: 1 jar of 6.
A. lunicollis: 1 jar of 10.
B. bipustulatus: 2 indivuduals.
C. fuscipes: 1 jar of 5.

Time (B.S.T.)	% activity			
	A. communis	A. lunicollis	B. bipustulatus	C. fuscipes
6 a.m.				
7				
8				
9				
10				
11	4.6			
12 noon				
1 p.m.	10.0			
2	13.6	15.8		12.5
3	24.0	5.1		6.25
4	20.0	20.5	9.0	
5	24.4	7.7		
6	20.0	12.8	14.4	
7	20.0	20.7	18.0	
8	12.9	14.6	14.4	
9	33.3	17.0	14.4	
10	30.2	32.8	83.3	38.7
11	41.5	44.0	75.0	71.0
12 m'night	60.7	45.7	56.2	90.47
1 a.m.	46.7	40.0	62.5	56.25
2	41.7	61.9	37.5	55.0
3	38.5	63.2	50.0	80.0
4	14.3	45.0	25.0	20.0
5	25.4	11.1	33.3	
6				

APPENDIX TABLE 29. August 1960.

C. violaceus: 3 individuals.

L. tericola: 3 individuals.

121 visits.

Time (B.S.T.)	% activity. C. violaceus	L. tericola
6 a.m.		
7		
8		
9		
10		
11		
12 noon		
1 p.m.		
2		
3		
4		
5		
6		
7		
8	4.8	
9	27.8	
10	91.7	58.3
11	66.7	85.7
12 m'night	66.7	58.3
1 a.m.	57.1	47.6
2	33.3	38.9
3	33.3	66.7
4	6.7	33.3
5		40.0
6		

SR 5.45 a.m. B.S.T.

SS 7.15 p.m. B.S.T.

APPENDIX TABLE 30. August 1960 (Continued)

C. fuscipes: 1 jar of 5.

C. melanocephalus: 1 jar of 5.

Time (B.S.T.)	% activity	
	C. fuscipes	C. melanocephalus
6 a.m.		
7		
8		
9		
10		
11		
12 noon	5.0	
1 p.m.	6.7	
2	6.7	
3	17.1	
4	13.3	
5	16.7	
6	11.4	
7	16.0	4.0
8	45.7	31.4
9	60.0	50.0
10	76.0	88.0
11	77.1	71.4
12 m'night	87.5	80.0
1 a.m.	82.9	71.4
2	70.0	66.7
3	25.0	80.0
4	20.0	73.3
5	20.0	86.7
6	10.0	60.0

APPENDIX TABLE 31. Vegetation and litter depths on beech litter plot. Summer 1960.

Trap	Litter depth (ins.)	Bracken	Ground layer	Field layer	Trap	Litter depth (ins.)	Bracken	Ground layer	Field layer
1	1.8		8	2	25	1.3		2	
2	2.1		9	1	26	1.3		3	
3	2.5		7	3	27	1.6		7	
4	2.6		5	4	28	1.7	5	5	
5	3.1		3	7	29	2.0	7	-	
6	3.6		3	9	30	1.4	1	5	
7	4.4		7	10	31	1.1		2	
8	3.0		10	7	32	1.3		1	
9	5.6		5	10	33	1.0		3	
10	6.2		3	6	34	1.1		6	
11	3.5		6	1	35	2.0	1	4	1
12	1.9		8	3	36	1.4	1	3	-
13	1.9		5	-	37	1.6	3	8	
14	1.7		8	-	38	1.0		5	
15	1.6	2	6	3	39	0.9		5	
16	1.0		7		40	0.9		8	
17	1.1		3		41	1.1	5	5	
18	1.4		3		42	3.2	9	-	
19	2.4		3	1	43	3.0	10	-	
20	3.8		8	4	44	2.9	9	1	
21	3.0		10	2	45	2.0	5	1	
22	3.7	3	10		46	1.8	4	-	
23	1.9		5		47	4.1	9	-	
24	1.3		1		48	3.0	9	-	
					49	3.5	10	-	

APPENDIX TABLE 32. Catches of *N. brevicollis* on Wood Bank beech litter plot. Autumn 1959.

Trap	Catch	Trap	Catch	Trap	Catch
1	5	25	10	49	9
2	21	26	21	50	30
3	10	17	12	51	44
4	4	28	8	52	21
5	12	29	14	53	32
6	7	30	24	54	44
7	13	31	12	55	81
8	9	32	8	56	21
9	14	33	15	57	62
10	4	34	35	58	71
11	19	35	50	59	48
12	20	36	19	60	3
13	5	37	9	61	7
14	18	38	9	62	27
15	18	39	11	63	50
16	22	40	34	64	3
17	26	41	5	65	14
18	9	42	19	66	20
19	16	43	25	67	-
20	30	44	55	68	8
21	25	45	58	69	10
22	27	46	10	70	16
23	6	47	34	71	14
24	9	48	48		

APPENDIX TABLE 33. Catches of Carabidae on beech litter plot. 3/5/60 - 25/11/60. (Only unmarked or dispersed adults included).

Trap	N. brevicollis adults	N. brevicollis callows	P. madidus adults	Abax adults	Abax larvae	C. piceus adults	Trap	N. brevicollis adults	N. brevicollis callows	P. madidus adults	Abax adults	Abax larvae	C. piceus adults
1	1		7	8	1	3	26	4			3		2
2	3		9	20	3	2	27	6		2	2	1	3
3	3		7	15	1		28	2		3	6		2
4	2		3	4	2		29	13		8	1	1	8
5	3		1	6	2		30	24	1	8		1	4
6			4	17		5	31	54		7			13
7	6		5	37	1		32	15	2	3	2		6
8	1		1	9	3	1	33	40	4	5			3
9			3	21	3		34	13	2	5	3		5
10			4	8		4	35	20		4	4		18
11	5		4	4		8	36	24	1	10	1	2	11
12	2		3	1	1	4	37	11		2	3	1	3
13	8		10	2		7	38	17	4	2	2	3	5
14	2		4	5	1		39	11	1		1		2
15	1		2	1			40	26	2	2		2	7
16	11	1	5			13	41			6	3	1	2
17	21		7			25	42	1	1	18	7		8
18	28		4	2	2	8	43			4	7	1	
19	7		4	2	1	11	44			1	6	1	
20	1		3	4		2	45	33	2	8	4		12
21			2	5	1	2	46	22	2	3	2		3
22	1	2	8	11		1	47	3	1	1	13		
23	9			1		5	48	1		1	10		
24	15		16	1		10	49			1	5		
25	8		7	2	2	13							

APPENDIX TABLE 34. Catch of marked *N. brevicollis* in three zones of beech litter plot. Autumn 1959.

Date	Total catch Zone			Release 1			2			3			4		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
28/9	102	-	-	-	-	-									
2/10	73	-	-	32	-	-									
3/10	39	24	59	16	4	6									
5/10	43	53	77	10	10	4									
7/10	28	22	38	4	2	3									
11/10	57	47	56	3	5	5	7	6	3						
13/10	99	99	86	6	8	8	5	7	8						
15/10	74	78	51	9	5	3	2	6	4						
22/10	57	84	88	4	5	6	7	5	3	15	15	11			
24/10	49	60	82	8	6	5	4	5	4	11	14	11			
26/10	39	81	73	5	1	7	3	5	0	10	5	7			
28/10	6	19	47	1	0	6	2	0	1	0	7	8			
2/11	15	13	26	1	0	0	1	2	1	3	3	5	4	3	3
4/11	14	30	47	0	1	5	2	1	4	2	5	8	3	7	0
7/11	3	21	44	1	2	2	0	0	4	0	4	7	1	2	1
10/11	2	11	13	1	1	1	0	0	1	0	5	1	1	1	1
13/11	0	2	6	0	0	0	0	0	1	0	0	0	0	0	2

APPENDIX TABLE 35. *Nebria* recaptures as % of total catch on beech litter plot. Autumn 1959.

Date	Release 1	2	3	4
5/10	8.0			
7/10	5.9			
11/10	4.4	5.7		
13/10	3.3	3.3		
15/10	5.3	1.9		
22/10	3.6	2.7	5.8	
24/10	4.7	2.1	9.8	
26/10	3.6	2.0	6.1	
(28/10	10.0	20.0	0)	
2/11	1.85	3.7	5.6	11.1
4/11	1.1	2.2	2.2	5.4
7/11	2.9	0	2.9	2.9
10/11	0	0	14.8	3.7

TABLE 36. Recaptures of *Nebria* expressed as % of total catch. Beech litter plot. Autumn 1960.

Date	Release 1	2	3	4	5	6	7	8	9	10	11
24/9	25.0										
26/9	40.0	0									
28/9	14.3	14.3	0								
30/9	22.7	13.6	13.6	0							
3/10	24.4	14.6	3.7	6.1							
5/10	27.6	15.5	1.7	1.7	12.1	15.5					
7/10	28.3	13.0	4.3	2.2	10.9	19.6	0				
13/10	8.3	8.3	0	8.3	16.7	50.0	8.3	0			
15/10	33.3	8.3	0	8.3	8.3	8.3	0	0			
18/10	17.1	17.1	4.9	2.4	0	26.8	4.9	4.9			
20/10	16.3	4.7	2.3	7.0	4.7	4.7	14.0	14.0	4.6		
24/10	18.3	6.7	3.3	5.0	5.0	16.7	3.3	6.7	11.7	13.3	
31/10	10.8	10.8	0	0	0	21.6	2.7	0	13.5	10.8	10.8
7/11	16.7	16.7	0	0	2.0	28.6	6.1	6.1	6.1	6.1	4.1

APPENDIX TABLE 37. % of population marked (all releases included) on beech litter plot. Autumn 1960. (Data from text table 44).

Date	Total catch	No. marked	% marked
24/9	32	8	25.0
26/9	10	4	40.0
28/9	7	2	28.6
30/9	22	11	50.0
3/10	82	43	52.4
5/10	58	43	74.1
7/10	46	36	78.3
13/10	12	12	100.0
15/10	12	8	75.0
18/10	41	32	78.0
20/10	43	31	72.1
24/10	60	54	90.0
31/10	37	30	81.1
7/11	49	42	85.7

APPENDIX TABLE 38. Mean temperature (grass minimum ^{o}F) and humidities (% 9 p.m.) (Silwood Screen records) during trapping periods. Autumn, 1959.

Date	Temp.	R.H.	Temp. x R.H.
3/10	46.25	61.5	2768
5/10	39.0	58.0	2262
7/10	34.25	55.5	1901
11/10	44.5	55.5	2470
13/10	38.25	60.5	2314
15/10	37.5	61.75	2316
22/10	38.5	59.75	2300
24/10	35.5	58.75	2009
26/10	33.75	59.0	1991
28/10	38.5	61.0	1963
2/11	34.5	60.25	2079
4/11	37.0	60.0	2220
7/11	26.7	68.0	1816
10/11	32.5	62.75	2039
13/11	25.8	60.0	1548

APPENDIX TABLE 39. Daily catches of N. brevicollis on beech litter plot Spring 1960.

Date	Period	Days	Catch	Mean daily catch	Callows	% callows
1-14/3	1	10	4	0.4	0	0
15-28/3	2	15	4	0.8	0	0
29/3-11/4	3	14	10	0.7	0	0
12-25/4	4	13	14	1.1	1	7.1
26/4-8/5	5	15	22	1.5	4	18.2
9-22/5	6	13	47	3.6	28	59.6
23/5-5/6	7	16	18	1.1	7	38.9
5-19/6	8	12	24	2.0	0	0
20/6-2/7	9	14	6	0.4	0	0

APPENDIX TABLE 40. Distribution of plant species and vegetation density. Elm Hill heath. 1960.

Trap	Holcus	Lotus	Galium	Stellaria	Density	Trap	Holcus	Lotus	Galium	Stellaria	Density
1	8	1	.	1	3.0	19	5	2		2	3.8
2	8			2	3.6	20	6	3	1	2	3.9
3	10				4.5	21	8	2			4.6
4	10				3.9	22	10	1	1	5	4.1
5	9		2	3	4.5	23	8		5	1	4.0
6	8		3	4	3.8	24	10		1		4.7
7	5	1	7	2	3.3	25	10		2		4.5
8	8		3	1	3.5	26	10	2	1		4.5
9	10			1	3.7	27	7		2		3.4
10	10			1	4.4	28	5	1			3.2
11	7	2	1	4	3.3	29	6			2	3.9
12	7	1		1	3.7	30	6			1	4.0
13	10				4.6	31	6		1	2	4.0
14	9			1	4.5	32	4	1		2	3.6
15	9			2	4.0	33	7	3		4	3.2
16	6		1	6	2.9	34	10	2			3.9
17	7	1		4	4.2	35	9				3.8
18	7		1		4.2	36	7				3.3

APPENDIX TABLE 41. Catches of *P. madidus* in Elm Hill heath plot. 25/7/60 - 15/9/60.

Trap	Catch	Trap	Catch
1	16	19	134
2	13	20	2
3	8	21	27
4	17	22	13
5	17	23	11
6	17	24	17
7	23	21	19
8	24	26	43
9	41	27	31
10	30	28	53
11	13	29	32
12	21	30	37
13	15	31	20
14	14	32	25
15	17	33	18
16	64	34	44
17	23	35	12
18	15	36	13

APPENDIX TABLE 42. Catches of P. madidus. Elm Hill heath plot. Summer 1960.

Period	Dates	Catch	No. traps	Days	Catch/36traps/day
8	June 6 - 19	9	24	10	1.35
9	June 20 - July 2	10	24	13	1.15
10	July 3 - 16	16 96	24 36	6 10	13.60
11	July 17 - 30	217	36	13	16.69
12	July 31 - Aug. 13	228	36	14	16.29
13	Aug. 14 - 27	253	36	14	18.07
14	Aug. 28 - Sept. 10	371	36	25	14.84
15	Sept. 11 - 25	20	36	9	2.22

APPENDIX TABLE 43. Marked P. madidus as a % of total catch. Elm Hill heath plot. 12/7/60 - 25/8/60. All releases combined and corrected to 100.

Days after release	Total catch	Corrected marked catch	% marked
0	517	34.1	6.6
4	695	33.5	4.8
8	561	24.3	4.3
12	332	6.7	2.0
16	343	6.1	1.8
20	190	0	0
24	127	0	0
28			

APPENDIX TABLE 44. Catches of *Amara* species and *A. parallelopipedus*. Elm Hill heath. Summer 1960.

2/6/60 - 12/7/60 (24 traps)			13/7/60 - 25/8/60 (36 traps)					
Trap	*A. communis*	*A. lunicollis*	Trap	*Abax*	*A. lunicollis*	Trap	*Abax*	*A. lunicollis*
7	1		1	1		19		
8	2	14	2		3	20		12
9		1	3		3	21		1
10		10	4		1	22		3
11		8	5		5	23		4
12	3	9	6		10	24		
13	2	6	7		1	25	3	1
14		12	8		11	26	1	7
15		2	9			27	1	15
16		5	10			28		6
17		1	11		3	29		5
18		1	12	1	1	30	1	2
19	1	1	13		3	31	2	1
20		3	14		5	32	4	
21	2	2	15		1	33	15	5
22		3	16		7	34	3	2
23	3	1	17		7	35	6	
24			18		13	36	1	
25	1	4						
26		4						
27								
28								
29		1						
30								