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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 16 APRIL 1965 PART VI

On the Ecology of some British Carabid Beetles with special Reference to Life Histories

By P. J. M. Greenslade

(Dept. of Agriculture, Honiara, British Solomon Islands Protectorate)

This account is based on work carried out at the Imperial College Field Station, Silwood Park, Berkshire, from 1958 to 1961 (in which certain aspects of the bionomics of 26 Carabid species were studied), supplemented by information on life histories made available to me from the theses of Dawson and Tipton, which are not readily accessible. Dawson (1957) studied small Fenland *Pterostichus* and *Agonum* species, and Tipton (1960), at Reading, worked on 22 Carabidae, of which six were not studied at Silwood. Gilbert's (1956, 1958) accounts of the life histories of *Nebria* and *Calathus* species in North Wales are also summarised in the present survey. A total of 43 species are considered and this includes the majority of the commonest Carabidae of lowland Britain.

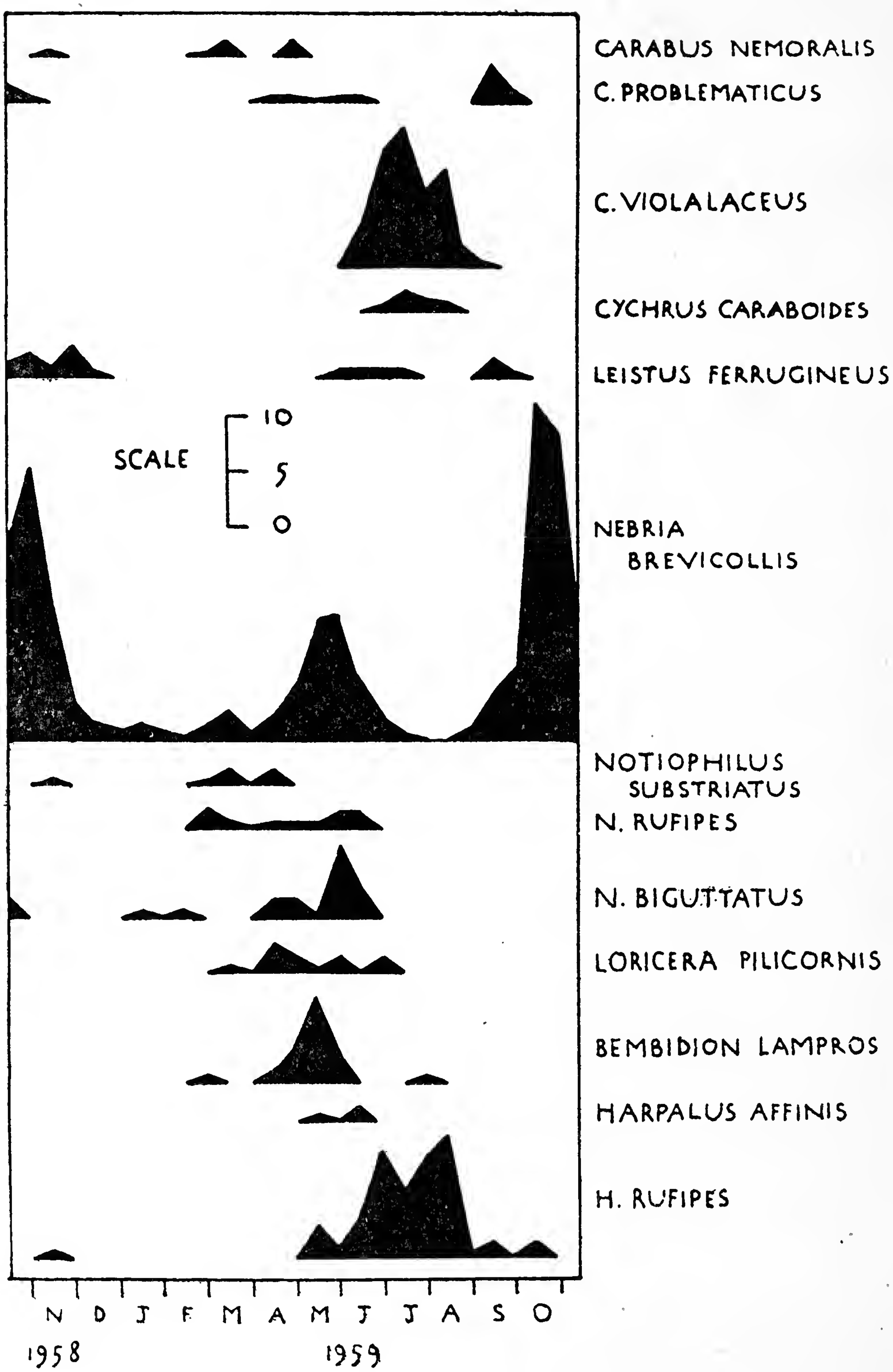
Outside the British Isles, Larsson (1939) described the life histories of Danish Carabidae, and his account was amplified for the rest of Scandinavia by Lindroth (1945-49). Geiler (1956-57) gives information on a number of German species. However, for any Carabid species these accounts are not necessarily applicable in Britain as there is evidence that life histories and other features show geographical variation within a species.

Larsson and Lindroth divide Carabidae into those which breed in the spring, have summer larvae and overwinter as adults, and those which spend the summer as adults, breed in the autumn and overwinter as larvae. This classification is used here.

In addition to the account of the life history, the habitat and, where known, daily activity cycle of each species are given in the following systematic account. They are subsequently discussed in relation to life history.

Methods

At Silwood Park, Carabidae were studied mainly by pitfall trapping. The life history accounts are based on records of adult abundance in traps and the occurrence of callows, combined where possible with records of copulation, the incidence of larvae and records of the overwintering stage; in some cases gonad dissections are made. Very similar methods were used by Tipton. Many Carabidae have resting periods in the adult state, and ideally pitfall trapping should be combined with some type of direct


CARABUS NEMORALIS
C. PROBLEMATICUS
C. VIOLALACEUS
CYCHRUS CARABOIDES
LEISTUS FERRUGINEUS
SCALE
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NOTIOPHILUS SUBSTRIATUS
N. RUFIPES
N. BIGUTTATUS
LORICERA PILICORNIS
BEMBIDION LAMPROS
HARPALUS AFFINIS
H. RUFIPES
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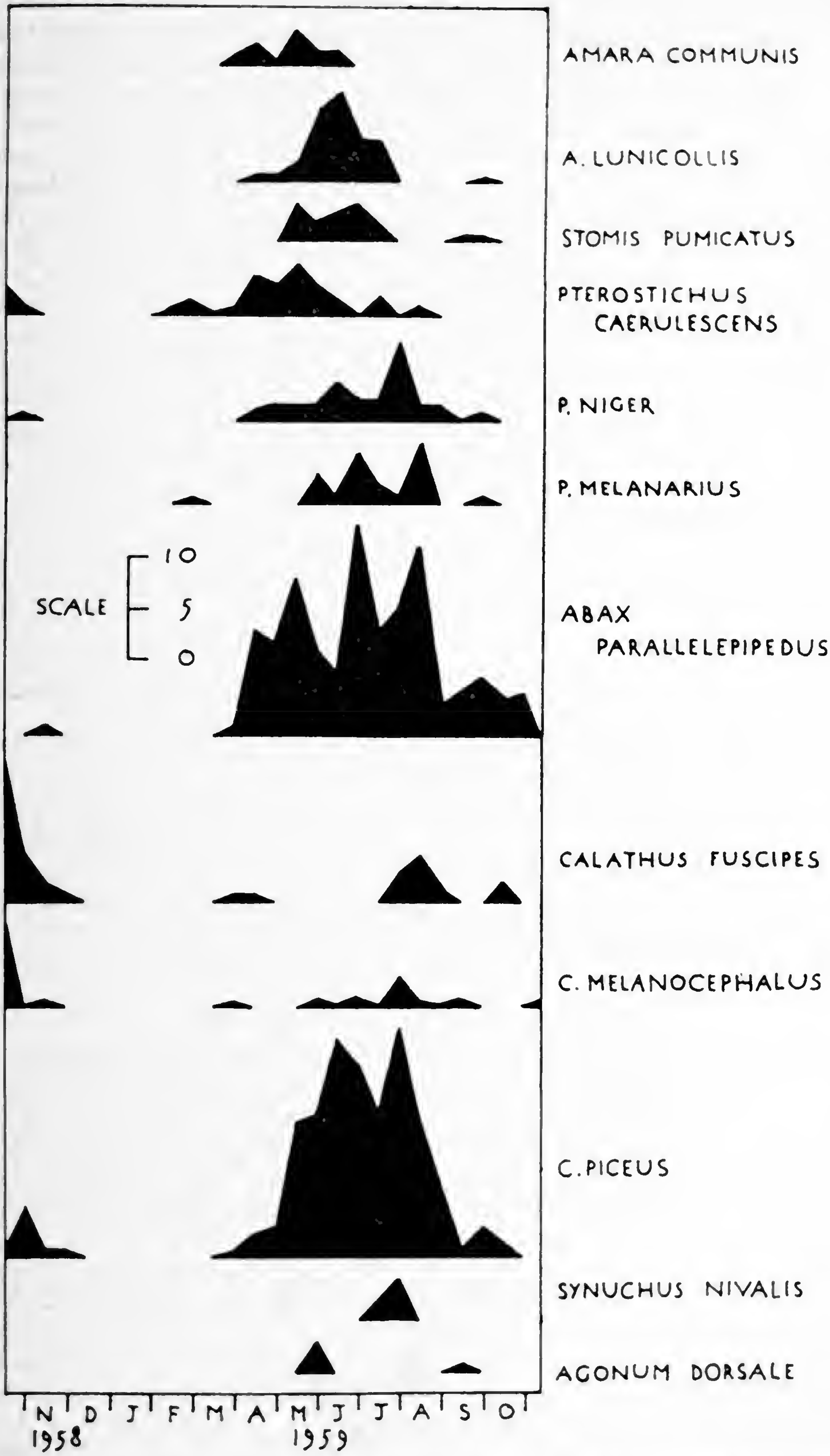

Fig. 1.—Fortnightly catches of Carabidae in 23 traps, on the Imperial College Field Station, 1958-1959: catches expressed as 10 × mean catch per day, except *N. brevicollis* where the actual mean daily catch is shown.

sampling to reveal inactive populations, as in Gilbert's (1956) and Dawson's work. However, many species are not amenable to such sampling. For example, *Nebria brevicollis* is seasonally one of the most abundant British Carabidae, and at times occurs in highly aggregated populations which may maintain the same pattern for long periods, but even so at Silwood the mean density within a natural population rarely exceeded one per square yard (Greenslade 1961). Twenty-three pitfall traps were visited as far as possible daily from October 1958 to November 1959, and from March to November 1960. To illustrate annual cycles of adult abundance the 1958-59 catches are shown in figure 1. In addition, up to 100 other traps were in operation, from time to time being visited at daily, or less frequent but regular, intervals. Details of the catches of these traps are recorded elsewhere (Greenslade 1961). The traps consisted of one pound jam-jars sunk in the ground, with a circle of radius of about one foot around each cleared of litter and vegetation.

Traps were situated in beechwood, bracken, grass heath and arable land. Two main groups of Carabidae were distinguished, those of woodland (beechwood and bracken), and grassland (arable and heath) (Greenslade 1963a). Of the species occurring in woodland 15 out of a total of 23 were studied, and in grassland 17 out of 54. Of these, six species were common to both habitats.

Greenslade (1963b) described three types of daily activity cycle in Carabidae, nocturnal, diurnal and plastic. The last include species whose patterns of activity vary from day to day according to weather, and also some which show geographical variation apparently in response to climate.

The life history accounts below are those described at the Imperial College Field Station unless explicit reference is made to other authorities.

Systematic Account of Life Histories

Carabus nemoralis Mull. (figure 1). 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 (1951) records two adult maxima also in Holland. Delkeskamp (1930) describes a cycle in Germany in which reproduction takes place early in the year followed by May-July aestivation by the spring adults, which show some autumn activity. Young imagines appear from July onwards and some may be mated in the autumn. The Silwood observations are in agreement with this cycle. Hikimiuk (1948) gives a similar account of the life history of this species near Moscow. In this case the active population of newly emerged adults in the autumn averaged only 70%, over four years, of the spring breeding population; this suggests that some adults are not active until the year following that in which they were larvae. In Sweden Lindroth's figures show a main peak in June, numbers falling in July with a slight increase in August.

At Silwood *C. nemoralis* occurred in grassland, although in Russia, Hikimiuk records it as a forest species. Observations on activity rhythms show this to be a nocturnal species in Britain, as it is in Germany (Kirchner, 1960), and Russia (Hikimiuk, 1948). Krumbiegel (1932), however, describes it as nocturnal in North and East Europe and diurnal in the South.

C. problematicus Hbst. (figure 1). 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. The life history has been described by van der Drift (1951): adults emerge in May and June, aestivate during the following two months and reappear to breed in the autumn. In south Sweden Lindroth records a single adult peak in July.

This is a woodland species but is characteristic of bracken and scrub on the edge of woodland rather than litter under intense shade within it. It is nocturnal.

C. violaceus L. (figure 1). 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. Tipton recorded a June-July maximum. This agrees with van der Drift's (1951) account in Holland where it is a larval overwintering species. 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. In Denmark the maximum occurs in June and July, and in Sweden from June to August.

At Silwood this was found to be a widely distributed, nocturnally active species, occurring in woodland, arable land and grass heath.

Cychrus caraboides (L.) (figure 1). Adults occurred at Silwood from June to September; no larvae were found. Tipton's records are similar. According to Lindroth this species overwinters as the larva, adults emerging and breeding from midsummer. It is a nocturnal, woodland species.

Leistus ferrugineus (L.) (figure 1). 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 brevicollis* with a late spring adult emergence, summer diapause, a main period of breeding in the autumn and larval overwintering. Lindroth found a single June maximum in Sweden, while in Denmark Larsson recorded two peaks, one in June and one in September.

L. ferrugineus is a woodland species occurring in the same habitats as *C. problematicus,* that is on the edge of canopied areas or in open woodland, rather than litter.

Nebria brevicollis (F.) (figure 1). The life history has been described in Britain by Gilbert (1956), and Williams (1959b). 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 which lasts from September until November.

At Silwood the life history was similar and is briefly summarised. Adults were trapped in the largest numbers in October and towards the end of the period mating occurred. First instar larvae appeared in laboratory cultures in November, and occurred in the field until April; later instars were found in traps and litter throughout the winter months and in early spring. In 1959 the first callow was recorded on 13th April and the rate of emergence is shown in table 1. About 20 days was required for newly emerged individuals to attain mature colouring and a hard integument on the dorsal surface. In the autumns of 1958-1960 occasional *N. brevicollis* were found which showed signs of immaturity on the under-side. They were probably late emerging or developing individuals from the spring and did not occur in sufficient numbers to invalidate the concept of spring emergence, summer diapause and autumn activity.

Table 1

Percentage of callow *Nebria brevicollis* adults in pitfall traps—April-June 1959

Trapping Period		Total Number of *Nebria*	Number of Callows	Percentage 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
,,	9-11	47	0	0
Totals		594	152	

At Silwood the spring catches were always lower than the autumn, but Williams (1959b) found that at Reading in one season spring catches were higher than those of the ensuing autumn. He cited 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 as describing a single peak. However, for Britain at least such records must be exceptional. Tipton concluded that all new adults left the pupal cell in spring but were active for only a short period, hence catches are generally lower than in the autumn. The same conclusion was reached from a population study at Silwood (Greenslade, 1961).

Tipton also found, again in agreement with Silwood observations, that some breeding continued throughout the winter. In connection with this the rôle of diapause in regulating the life history is discussed later.

Tipton found similar numbers of each sex in traps during the spring emergence, and a ratio of two males to one female in the autumn. At Silwood where allowance was made for disturbance activity due to the marking and recapture method used (Greenslade, 1961), it was found that male locomotor activity exceeded that of the females in the ratio 1·5 : 1 in the autumn, and that the absolute populations of each sex were equal; thus the males are relatively more active in the breeding season.

Although populations extend into other habitats, *N. brevicollis* is essentially an inhabitant of woodland litter, and is nocturnal.

According to Gilbert (1958) the life history of *Nebria salina* Fairmaire & Laboulbene, is essentially the same as that of *N. brevicollis.*

Notiophilus substriatus Waterh. (figure 1). Although catches of adults were low, they suggest a life history similar to those of *Notiophilus biguttatus* and *N. rufipes.* 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. 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 (1955) mentions that some small diurnal Carabid species are bivoltine and *N. substriatus* may be one of these.

N. substriatus is diurnal, and was found in woodland and grassland.

Notiophilus biguttatus (F.) (figure 1). 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 a collection from Silwood larvae were distributed as follows: 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.

This species is a diurnal inhabitant of woodland litter.

N. rufipes Curt. (figure 1). The life history is the same as that of *N. biguttatus,* there being early summer and autumn peaks of adult activity. Although no larvae were 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 and Davies (1959), and Williams (1959b) 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*.

It is a diurnal woodland species, and of the Carabidae considered here is the one most narrowly restricted to litter.

Loricera pilicornis Latr. (figure 1). Adults were trapped from February to August with a maximum in April and May. Larvae were recorded from May to July. Tipton found an April maximum, a midsummer decline and a slight increase in the autumn. Similarly Larsson recorded April-May and July-August maxima. However, in Sweden, Lindroth describes the species as overwintering as the adult with a single peak of activity. In central Germany Geiler (1960) records a single peak from May to July. In Britain the life history would seem to consist of overwintering by adults which breed in the following spring. Some of these adults may survive through the summer. Newly emerged imagines show some activity in the autumn.

Loricera was found to be diurnal at Silwood, but Kirchner (1960) records nocturnal activity in western Germany. This species occurs in a wide range of habitats (at Silwood in beechwood, alder carr, and on arable land), and it is possible that the daily time of activity varies with microclimates of different habitats.

Clivina fossor (L.). This species was studied by Tipton who describes it as overwintering as the adult, and breeding in the spring with maximum catches in April and May. It has been taken at Silwood and elsewhere in pasture and on the edge of woodland. It is most probably nocturnal.

Bembidion lampros (Hbst.) (figure 1). Adults were 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.

It is a diurnal species typical of arable fields, but is also common in grassland.

Harpalus affinis (Schrank) (figure 1). Adults occurred 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 were found from June to October. According to Briggs (1957) the life history is similar to that of *H. rufipes* which follows. It should be noted that in Czechoslovakia, Skuhravy's (1959) results suggest that *H. affinis* shows a June maximum, a decline in July and August and slight increase in October, while in *H. rufipes* a simple August maximum occurred.

At Silwood *H. affinis* occurred most abundantly on arable land, but was also common in grass heath. It was found to be nocturnal under experimental conditions, but diurnal activity was frequently observed in the field. Here it is defined as plastic in its daily activity.

H. rufipes (Deg.) (figure 1). 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; some of the resulting larvae are adults by the autumn, but do not breed until the following summer. The majority overwinter as larvae and produce callow adults early in the year. Briggs (1961) compared pitfall catches and populations shown by direct sampling in this species. Absolute numbers were highest in June and July although pitfall catches were greatest before and after this period in May and in late July and August. The early peak in catches can be attributed to activity by overwintering adults, and the later catch maximum to adults which had emerged earlier that summer. Rather high total numbers and low catches in early June suggest that the newly emerged generation shows less activity when callow than when mature.

Both this and the preceding species are clearly autumn breeders and larval overwinterers, but there is room for further observation on the amount of adult overwintering which occurs. *H. rufipes* is essentially an arable land species and is nocturnal.

Amara plebeja (Gyll.). Tipton found a May maximum with some catches in September. In Denmark and Sweden single maxima in, respectively, June-July, and June, are recorded. It overwinters as the adult and breeds in the spring. A grassland species, it is normally diurnal but may be plastic in its daily activity.

Amara communis (Pz.) (figure 1). Adults were trapped from March to July with a peak in late May and early June; callows were active in September. Large numbers of *Amara* larvae were taken but it is not possible to determine their identity further than the sub-genus. Lindroth considers it is 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.

This species was typical of grass heath, being absent from woodland habitats and infrequent on arable land. It is plastic in its daily time of activity.

A. lunicollis Schdt. (figure 1). 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 were taken in September. Again this is an adult overwintering species differ-ing from *A. communis* only in having an adult maximum later by approximately one month.

In habitat and activity time this species is the same as *A. communis*.

Stomis pumicatus (Pz.) (figure 1). 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.

It is a woodland species especially of bracken and open woodland, and is nocturnal.

Pterostichus cupreus (L.). This species was studied by Tipton who recorded March-April, and October maxima in pitfalls. In Denmark a May maximum is found with a small increase in September; in Sweden only a May peak occurs. In Britain this is evidently an adult overwintering species breeding in the spring, at least some of the new adult generation being active in the autumn.

P. cupreus is a diurnally active inhabitant of grassland.

P. caerulescens (L.) (figure 1). This species was considered in detail by Tipton. At Silwood it 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 the autumn, which in 1960 exceeded the earlier maximum. No larvae were taken but overwintering adults were found. From this it would appear that like *P. cupreus* this is a spring breeder with winter adults, and a larval period lasting from May-June until August-September. Tipton's account is in agreement with this. Lindroth recorded a single May-June maximum in Sweden, and Larsson in Denmark a main May peak with a smaller one in August.

Tipton found that the fat body of the adult increased during the six weeks or so of post-emergence activity, in the autumn, but the gonads did not mature until the spring. Experiment showed that this was not due to low winter temperatures, and it was suggested that some physiological mechanism was responsible.

P. vernalis (Pz.). This species was studied by both Tipton and Dawson whose accounts are combined here. It overwinters as the adult and breeds in the spring. Adults show maximum activity early in the year between April and June when eggs are laid. Newly emerged callows are active in the autumn from September onwards before retiring to hibernation sites. In Denmark there are April and September maxima and in Sweden a simple June maximum.

P. vernalis is found in fens, carr and badly drained grassland, and is most probably nocturnal.

P. niger (Schall.) (figure 1). Adults were 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 were recorded. Van der Drift (1951) 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 that it is an autumn breeding species with 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.

This is a widespread species occurring in woodland and grassland, but less frequently on arable land. It is nocturnal.

P. melanarius (Ill.) (figure 1). This species was trapped from February to 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. Pupae occur in May and the new generation of imagines appears in June. Although primarily a larval overwintering species, some adults may hibernate. This observation was also made by both Larsson and Lindroth, and gonad dissections by Tipton suggested that some individuals may breed in a second season.

It is a nocturnal species of grassland and arable fields.

P. nigrita (F.). The following is Tipton's account. It overwinters as the adult with March-April and October maxima. In Denmark there are April-May, and August-October maxima, and in Sweden a single May-June peak.

This species is nocturnal and occurs in damp places.

P. minor Gyll. The account of the life history of this and the two following species is due to Dawson. The cycle is similar to that of *P. vernalis*. The overwintering stage is the adult and larvae occur in July and August; breeding activity takes place from April to July, and newly emerged adults are active from August to November.

It is an inhabitant of damp and often shady places and is most probably nocturnal.

P. strenuus (Pz.) and *P. diligens* Sturm. In both these species the life history is basically the same as in *P. vernalis* and *P. minor*, with overwintering adults, spring breeding, and summer larvae. Adults are active from April onwards, but the two species differ in that the new generation of *P. diligens* adults is active as early as July, while in *P. strenuus* they do not appear until August.

Both are species of damp places, and although the daily time of activity is not known, they are probably nocturnal.

P. madidus (F.). Pitfall catches of adults in 1958-59 are shown in figure 2: they were present almost throughout the year with a well-marked peak during July and August, when copulation was frequent. Catches fell during the winter, reaching a minimum in February and March.

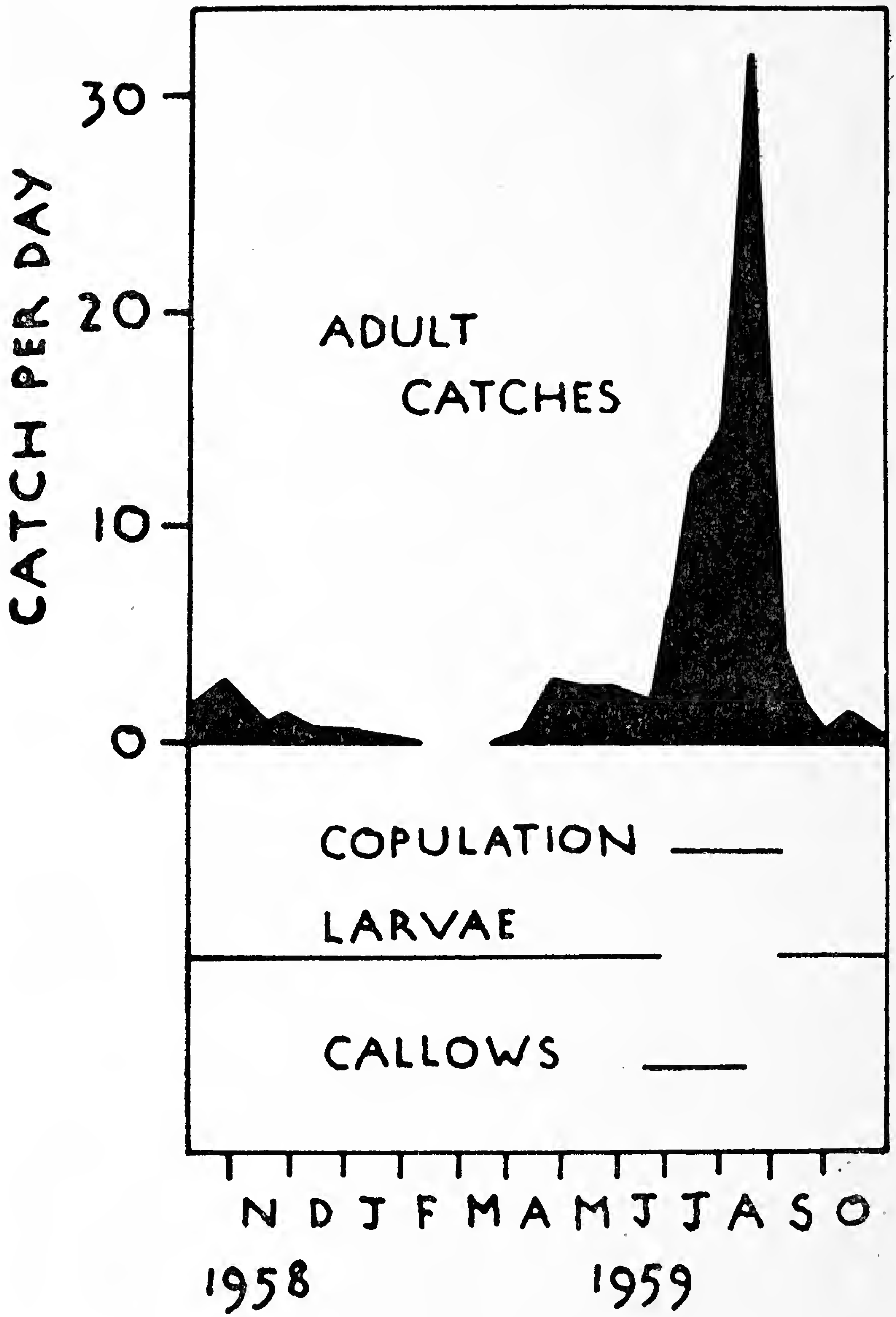

Fig. 2.—Life history of *Pterostichus madidus* showing mean daily catches of adults in 23 traps on the Imperial College Field Station, 1958-59, and the incidence of copulation, larvae and callows.

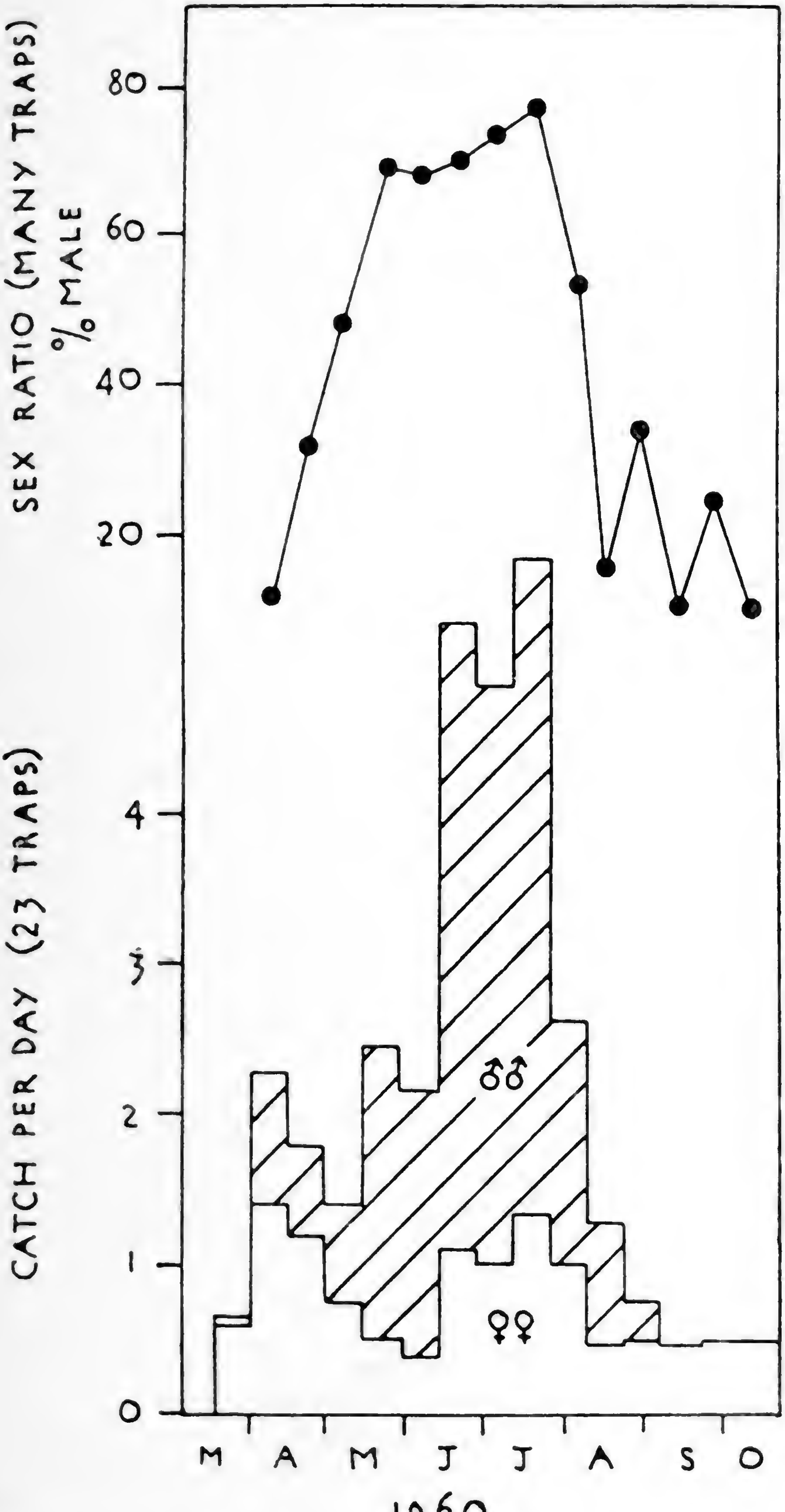

Fig. 3.—*Pterostichus madidus*: changes in the sex ratio, 1960.

Larvae of this species were found only infrequently in traps, but they were recorded in soil 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.

In 1960 changes in the sex ratio were determined in those *P. madidus* taken in a large number of pitfalls as shown in figure 3, also included are the mean daily catches of male and female *P. madidus* in the 23 traps. 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 4 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.

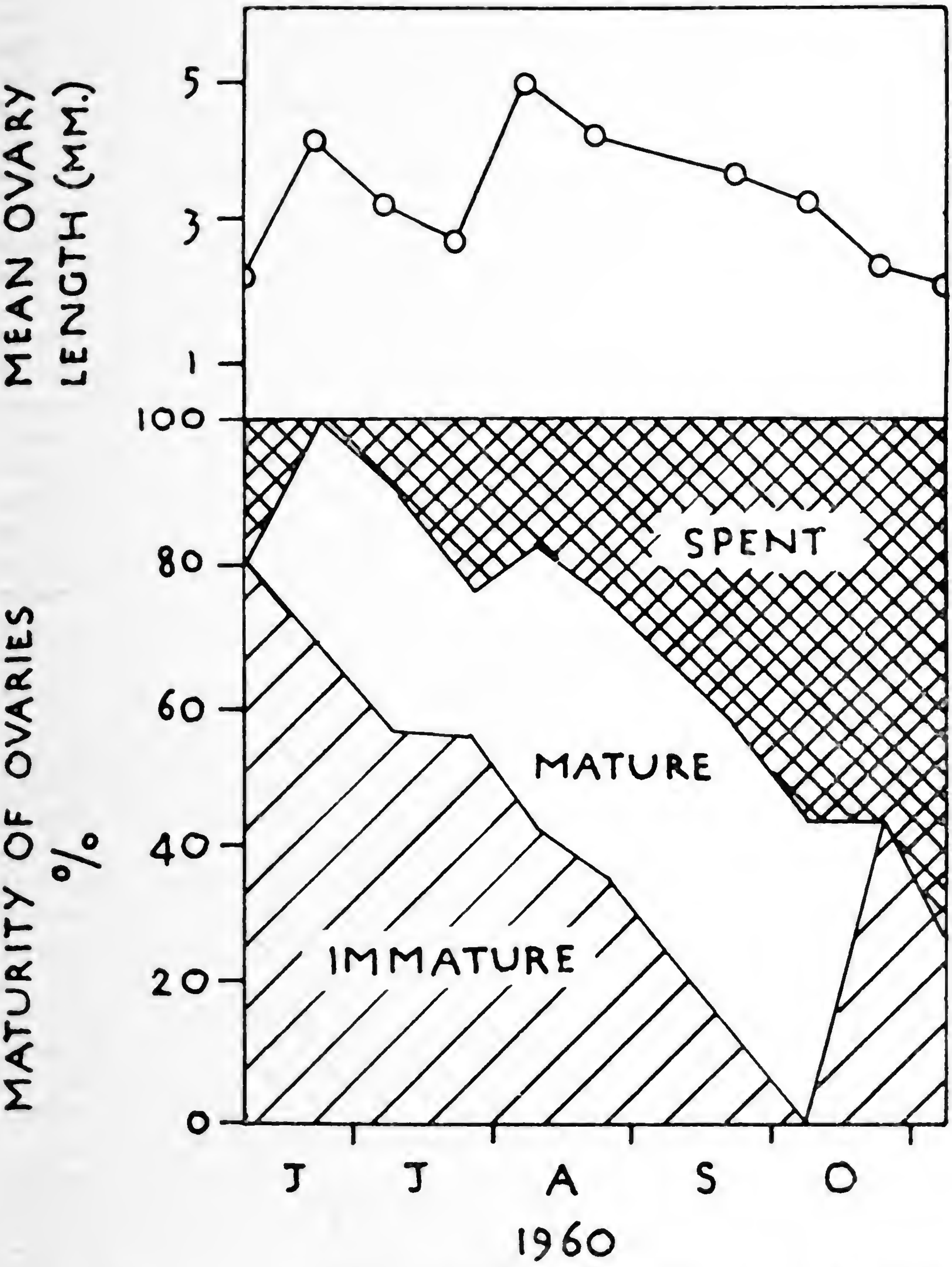

Fig. 4.—*Pterostichus madidus*: condition of the ovaries in 134 females dissected in 1960; above, average ovary length; below, the percentage composition of the population on different occasions in terms of the state of maturity of the ovaries.

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%. 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 had 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. In this work 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.

Tipton's (1960) dissections of a small number of adult *P. madidus* of both sexes suggested that for the main summer emergence the gonads mature more rapidly in the males than in the females. If this normally occurs it will allow early fertilisation of overwintering females by the first males to appear.

P. madidus is widely distributed in woodland and grassland but is most frequent in the latter. It is plastic in its daily activity rhythm tending to be diurnal in grassland, and nocturnal in woodland (Williams, 1959b, Greenslade, 1963b).

Abax parallelepipedus (Pill. & Mitt.) (figure 1). At Silwood 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 under logs and in litter.

The sex ratio in traps in two week periods in 1960 are shown in table 2.

TABLE 2

Sex ratio of *Abax parallelepipedus* in traps, 1960 (%)

Month	May		June		July		Aug.		Sept.		Oct.	
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 also 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 2 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 percentatge 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.

Abax parallelepipedus is a woodland species most frequent in bracken and scrub rather than bare litter. It is nocturnal.

Calathus fuscipes (Gz.) (figure 1) and *C. erratus* Sahl. Adults of *C. fuscipes* were trapped most commonly at Silwood from July to October, although occasional specimens were taken throughout the year. The life histories of this species and *C. erratus* are described by Gilbert (1956) in North Wales, and are apparently similar. The account summarised here applies specifically to *C. erratus*.

Larvae overwinter and breeding takes place in the following summer. Callows appear in May and June with maximum adult activity in July and August. Egg laying begins in July and may continue until the end of October. The winter is spent in the third larval instar. A state of pre-pupal torpor was recorded in larvae, being entered from January to April. In both species some adults may breed in two seasons.

C. fuscipes is a nocturnal grassland species. Gilbert's observations suggest that *C. erratus* is also nocturnal. Both species occur in the same type of habitat, but Lindroth (1945) suggests that *C. erratus* requires a soil with a higher calcium content.

C. melanocephalus (L.) (figure 1) and *C. mollis* (Marsh.). At Silwood the life history of *C. melanocephalus* was found to be very broadly the same as that of *C. fuscipes*. *C. melanocephalus* and *C. mollis* were also investigated by Gilbert who found them to be similar, but showed that there were some differences between the preceding pair. Again his account is cited.

The adult maximum occurs in September and October and larvae overwinter. In all four species pupation occurs in April and early May, but the two species pairs differ in the time by which the gonads are mature. In *C. erratus* and *C. fuscipes* adults are all mature by August, while in the other two species complete maturity is not reached until September.

In *C. mollis* and in *C. melanocephalus* all larval instars were present during the winter. In *C. mollis* there is evidence that individuals may breed in two seasons.

C. melanocephalus is a nocturnal species of grassland, although it occurs in a variety of habitats from sand dunes to conditions which are almost montane. *C. mollis,* also nocturnal, is restricted to sandy habitats.

C. piceus (Marsh.) (figure 1). 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 and in Denmark has an August-September maximum.

C. piceus occurs in the same woodland litter habitats as *Nebria brevicollis*; it is nocturnal.

Synuchus nivalis (Pz.) (figure 1). 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.

Synuchus occurred in the edge of woodland, in bracken and scrub, and in grassland. It is nocturnal.

Agonum muelleri (Herbst). Tipton found this species to be a spring breeder with overwintering adults; maxima occur in May, and August-September.

It has a wide habitat range occurring in damp places but also in arable fields on very dry, sandy soil. Overwintering adults are common under bark and in other refuges in woodland. It is plastic in its daily activity.

Agonum dorsale (Pont.) (figure 1). This species 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 this 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 South Sweden show a June maximum and a slight increase in numbers in September. Geiler (1960) recorded July maxima in traps in central Germany.

A grass and arable land species particularly common in calcareous localities; daily activity is plastic.

Agonum viduum (Pz.), *A. obscurum* (Hbst.), *A. fuliginosum* (Pz.), and *A. thoreyi* Dej. These four species were studied by Dawson. They occur in damp habitats and their daily rhythms of activity are undescribed. All overwinter as adults, breeding in the summer. They differ mainly in the timing of the adult maxima.

Adults of *A. obscurum* occur throughout the summer; breeding last from June until August, and callows emerge from September until the end of November.

A. fuliginosum adults breed earlier in the year in May and June, and callows appear from August onwards.

A. thoreyi resembles *A. obscurum,* breeding in June and July.

A. viduum breeds from May to July, but callows only emerge from mid-June until the end of September.

Discussion

Classification of Life History types

The systematic account shows that the distinction between adult and larval overwintering species holds good for almost all the Carabidae included. The only real exceptions are the larval overwintering *Harpalus rufipes* and *Abax parallelepipedus* in which a degree of adult overwintering occurs. In both cases this appears to be due to some adults breeding early in the summer. The resulting callows are active in the autumn of the same year and overwinter as adults. To a much lesser extent this also occurs in other larval overwintering species, for example *Pterostichus madidus.* In addition, in many of these species some adults which have bred survive to enter the winter and may breed again in the following season. However, the initial division on the bases of the main overwintering stage remains valid, but there are differences between species within these two life history groups.

In the larval overwintering species, apart from variation in the extent to which winter adults occur, there is an obvious division between those species with two annual maxima, *Carabus problematicus, Leistus ferrugineus,* and *Nebria brevicollis,* and the remainder with one maximum. Similarly among the adult overwintering species some habitually show a bimodal curve of annual adult activity, for example *Carabus nemoralis, Pterostichus cupreus, P. vernalis* and *Agonum fuliginosum*; others, for example *Notiophilus* species and *Bembidion lampros* tend to occur as adults throughout the summer with only a slight autumn increase in catches to indicate the emergence of young imagines. However, there is a complete range between these extremes, and also the amount of autumn activity may vary from year to year.

The catches of adult overwintering species in certain traps at Silwood in 1959 and 1960 are shown in Table 3.

TABLE 3

Catches of adult overwintering species, 1959-60

	1959	1960
Total catch	156	126
Catch from August onwards	5	35
Early Summer catch	151	91

In the species concerned, the autumn emergence occurred in August and September and catches from then onwards can be subtracted from the annual total; the remaining catches are those made during the breeding maximum. This shows that there was relatively very much more autumn activity in 1960 than in the previous year.

The Carabidae studied at Silwood Park fell into several groups according to the time of maximum annual adult activity. In figure 5, records from pitfall traps are summarised, showing the

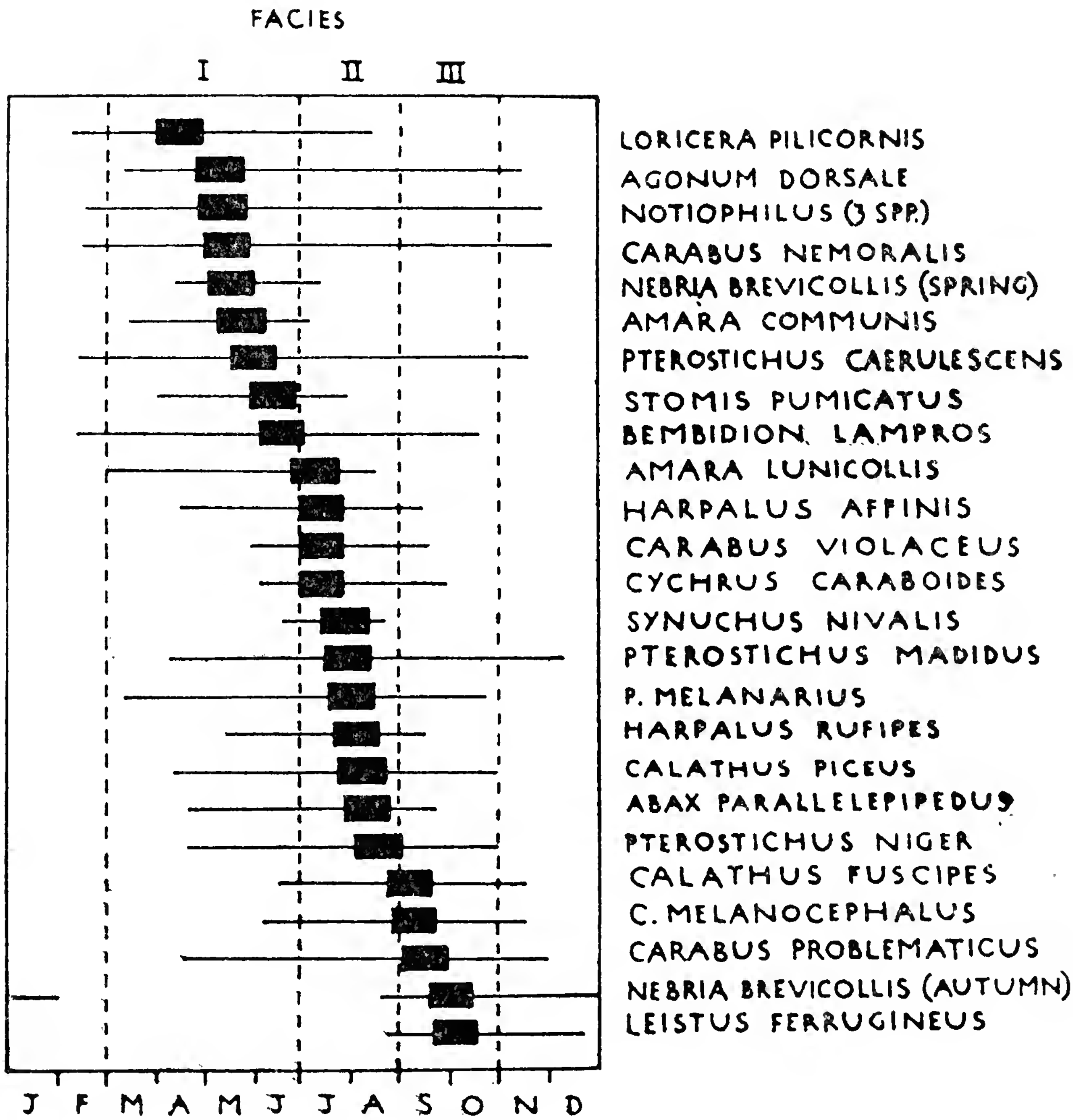

Fig. 5.—Annual distribution of locomotor activity in Carabidae from pitfall catches; horizontal lines: periods when species were frequent in traps; blocks: months of maximum catches.

month of maximum frequency for each species, and, also, on the basis of the experience of three years' trapping, the period in which more than occasional individuals occurred. In those species with two maxima, the one immediately following emergence is only shown for *N. brevicollis*.

The maxima show a succession through the year but three seasonal facies can be distinguished.

I. March-June:—*Loricera pilicornis, Agonum dorsale, Carabus nemoralis, Amara communis, Notiophilus* 3 spp., *Stomis pumicatus, Nebria brevicollis* (spring emergence), *Bembidion lampros, Pterostichus caerulescens.*

II. July and August:—*Amara lunicollis, Harpalus rufipes, H. affinis, Carabus violaceus, Synuchus nivalis, Pterostichus melanarius, Calathus piceus, Abax parallelepipedus, Pterostichus niger, Cychrus caraboides, Pterostichus madidus.*

III. September and October:—*Calathus fuscipes, C. melanocephalus, Carabus problematicus, Nebria brevicollis* (autumn breeding season), *Leistus 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 was characterised by the trapping of *Stomis* and *Amara communis,* and newly-emerged *N. brevicollis* are also abundant. As *A. communis* declined, *A. lunicollis* appeared in numbers and defined 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* disappeared from traps in late August there was 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 *N. brevicollis* 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 were either survivors of the summer and autumn facies, *P. madidus, N. brevicollis, 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 occurred, with the adult overwintering species *Loricera, C. nemoralis, Notiophilus* species, *B. lampros* and *P. caerulescens*; of these, two out of nine species (22%) overwinter as larvae.

The percentage of larval overwintering species in each facies may also be compared (table 4).

Table 4

Incidence of larval overwintering species in seasonal facies

Facies	No. spp.	No. larval over-wintering spp.	% larval overwintering
I Spring	11	1	9
II Summer	11	10	91
III Autumn	5	5	100

From November to February the species were selected by their relative abundance in traps within a given period, and the percentage figures are not strictly comparable with those for March to October where species are placed in a facies, according to their maxima 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 show a reversal of the trend with the autumn emergence of adults of spring-breeding species, which by January and February predominate.

Carabidae and the microclimate

The basis of the argument outlined here is that in the areas and habitats considered and within normal climatic limits, both high temperatures and high humidities are favourable to Carabidae. Mellanby (1939, 1940, 1958), Williams (1940), Falconer (1945), Nicholson (1934), Wigglesworth (1953), Colhoun (1960) and others show that activity and rates of development in insects increase with increase in temperature. This is not a simple relationship as there are conditioning effects. That locomotor activity in Carabidae varies with temperature has been demonstrated from pitfall captures by Briggs (1961) and Greenslade (1961). Williams and Osman (1960) suggest that in Northern Europe temperatures rarely even reach the optimum for insect species.

Tipton (1960) and Kless (1961) showed that many Carabidae require a high humidity, by relating the habitats of certain species to the humidities they preferred and tolerated; Hamilton (1917) and Kern (1912) noted that Carabid larvae were more susceptible to desiccation than the adults.

The temperature and humidity of the Carabid environment commonly vary inversely, so that to enjoy a high value of one a low value of the other must be endured. The profound effect of low winter temperatures on the annual cycles of insects in Northern Europe shows that temperature is generally the most important.

Thus for those species which can endure low humidity, habitats with higher temperatures are the most favourable.

A comparison of woodland and grassland shows the differences in temperature and humidity between sheltered and open habitats.

Observations recorded by Geiger (1959), MacFadyen (1957) and others demonstrate that a cover of vegetation lowers mean temperatures at ground level and reduces and retards the daily and seasonal fluctuation, in comparison with more open habitats. On the Imperial College Field Station in August 1960 it was found that in woodland and grassland the minimum temperatures reached at the soil surface were the same but maximum temperatures in the latter were 5-7°C. higher than in woodland. In grassland the maximum was reached between noon and 4 p.m. (G.M.T.) but in woodland not until some six hours later. Similar temperature differences were noted by Tischler in a comparison of heavy and light soils (1955). In some types of habitat, however, high temperatures and humidities are associated, especially where stones or other cover under which humidity is high, are scattered on bare ground. Here large concentrations of Carabidae, both individuals and species, have been recorded (Greenslade, 1963c).

The Carabidae studied at the Imperial College Field Station were divided among woodland (litter and bracken), grassland (arable and grass heath), and widely distributed species (Greenslade, 1963a). These habitats were part of the temporal vegetation succession:—Bare ground→ Weed cover→ Grass heath→ Scrub→ Oakwood→ Beechwood. Here arable land stands for the initial stages and bracken for scrub as it is typical of this stage. Tischler (1955) considered that in some cases soil type was more important than the vegetation cover in determining Carabid distributions, but in this case where all stages of the succession occurred on the same soil type this does not apply. Williams (1959a) suggested that the richness of the edaphic fauna was governed by litter development. Again this does not agree with the Carabidae of the habitats investigated at Silwood Park. A total of 16 species were described as woodland, and 49 as grassland species, while seven were generally distributed. Thus the richest Carabid fauna was found where litter development was least. Therefore it was concluded that microclimates associated with different types of vegetation were the most important factor determining the occurrence of Carabidae.

Habitat and Activity

The relationship between different habitats, that is their microclimate properties, and daily and annual cycles of activity in Carabidae can be examined. If locomotor activity in Carabids is governed mainly by temperature it is evident that open habitats will favour diurnal activity, and sheltered ones nocturnal. In those species which are limited by humidity, activity in open habitats will tend to be restricted to the night. In agreement with this, Williams (1959a) found more diurnal activity in Carabidae in open scrub than in closed canopy woodland. Similarly Tischler (1955) recorded more diurnalism on sandy than on heavy soils; it was also noted that on the former nocturnal activity was greatly reduced on cold nights. This can be further illustrated by the Silwood results. The life histories and habitats of species and their activity cycles are shown in Table 5, which summarises the systematic account. In the 26 species included there is relatively more diurnal activity in the species from grassland habitats than those from woodland, for those which are plastic will tend to be diurnal in grassland and nocturnal in woodland, as in *Pterostichus madidus* (Williams 1959b, Greenslade 1963b). If the widespread species are added to both major habitat groups, the distribution of activity times in the species from each is:—woodland, 12 nocturnal and 3 diurnal species, and grassland, 8 nocturnal and 9 diurnal. It must be pointed out that the species studied at Silwood Park represented neither complete nor

TABLE 5

Summary of habitat, activity and life history of Carabid species

Species	Habitat	Daily Activity	Annual Activity	Overwintering stage
Notiophilus rufipes		D	S	a
Calathus piceus		N	M	l
Nebria brevicollis	L	N	A	l
Cychrus caraboides		N	M	l
Notiophilus biguttatus		D	S	a
Abax parallelepipedus		N	M	l
Carabus problematicus	B	N	A	l
Leistus ferrugineus		N	A	l
Stomis pumicatus		N	M	a
Pterostichus niger		N	M	l
Carabus violaceus		N	M	l
Synuchus nivalis		N	M	l
Loricera pilicornis	W	P	S	a
Notiophilus substriatus		D	S	a
Pterostichus madidus		P	M	l
Carabus nemoralis		N	S	a
Amara communis		P	S	a
A. lunicollis	H	P	M	a
Calathus fuscipes		N	A	l
C. melanocephalus		N	A	l
Harpalus rufipes		N	M	l
H. affinis		P	M	l
Pterostichus caerulescens		D	S	a
Bembidion lampros	A	D	S	a
Pterostichus melanarius		N	M	l
Agonum 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 = larva

random samples of the species present in each habitat. However, there were 16 woodland species of which nine were studied, while in the grassland habitats there were 49 species of which 11 are included here. Of the other grassland species *Amara plebeja* and *Pterostichus cupreus* are mentioned in the systematic account and are diurnal as is *Asaphidion flavipes* (L.), another grassland species (Greenslade 1963b). Also in grassland in the area studied, 18 species of *Amara* occurred; many of these possessed a brassy metallic integument, and Tischler (1955) noted that this was associated with diurnalism.

Habitat and overwintering can also be related. Of the woodland species, one-third (3/9) overwintering as adults and the number of species belonging to the spring, summer and autumn facies are respectively 2:4:3. In contrast, more than half the grassland species overwinter as adults (6/11) and the spring, summer, autumn proportions are 5:4:2. Table 5 also shows a close relation between overwintering stage and activity times; diurnalism, adult overwintering and activity early in the year tend to be associated, and conversely, late summer and nocturnal activity and winter larvae.

As the species studied were not necessarily representative of the Carabid fauna of the different habitats one cannot relate the number of species of various activity types directly to habitat. But in any species the daily time of activity is often associated with a characteristic annual periodicity. As there is independent evidence that the woodland type of microclimate is associated with nocturnalism, and the grassland with diurnalism, one can conclude that in woodland habitats, nocturnalism, winter larvae, and late summer activity predominate, while in grassland there is more diurnalism, activity earlier in the year, and adult overwintering.

Geographical variation

It has been suggested that in South East England Carabid habitats and activity cycles are related. In a species any of these characteristics may vary geographically, especially life history, and this can be attributed to climate. The obvious differences in a North-South direction are higher mean temperatures and longer summers in the South, and Tipton (1960) compares monthly mean temperatures at Greenwich, Copenhagen and Uppsala. In each, July means lie between 17 and 18°C., while the January temperatures are Greenwich 4·4°C., Copenhagen 0·8° C., and Uppsala −2·8°C., the March means are respectively 6·2° C., 2·3°C., and 1·3°C. The East-West trend is from an Eastern Continental climate with a great difference between winter and summer temperatures, to an Atlantic one with milder winters. In this direction the annual differences are similar to the daily ones when woodland and grassland are compared. In woodland, corresponding to an Atlantic climate, the amplitude of fluctuation is least and humidities are higher.

For life histories the Atlantic-Continental transition is from a large proportion of larval overwintering species in the West to adult overwintering in the East. This was pointed out by Lindroth (1945) who cited as an example *Calathus melanocephalus* which overwinters as the larva in Britain but as the adult further East in Europe. Here the predominance of winter larvae in an Atlantic climate can be equated with their frequency in woodland. In other species the life history shows no East-West change but different habitats are occupied. Thus *Carabus nemoralis* has the same annual cycle in Britain and Russia, but in the former occurs in open habitats and in Russia in forest (Hikimiuk, 1948). On the other hand *Loricera pilicornis* and *Pterostichus madidus* which are nocturnal in open habitats in Germany (Kirchner, 1960) are diurnal in the same type of habitat in England. It can be suggested that diurnalism and the occupation of open habitats, with the advantage of higher temperatures and hence also higher levels of activity, are permitted by higher humidities in Atlantic Britain.

In a North-South direction the situation is simpler, at least so far as Scandinavia and Southern Britain are concerned (further South in Europe information on life histories is scanty). In England spring breeding occurs earlier, and breeding continues later into the autumn, and this can be related to temperature. The shorter Northern summer also leads to the double maxima of adult activity found in many English Carabids, contracting to a single maximum in Sweden, to which two generations contribute. The situation in Denmark is usually intermediate. Larval overwintering species in which two maxima become one further North are *Carabus problematicus, Leistus ferrugineus* and *Nebria brevicollis;* adult overwinterers include *Loricera pilicornis, Amara communis, Pterostichus cupreus, P. caerulescens, P. vernalis* and *P. nigrita.*

Regulation of Life Histories

Very little work has been carried out on the regulation of annual cycles in Carabidae or on the importance of diapause, but some observations are made here and preliminary conclusions drawn from them.

Some Carabid species show distinct and restricted annual peaks of adult activity, examples being *Pterostichus madidus* and *Nebria brevicollis,* while other species such as *Abax parallelepipedus* are active throughout the warmer months of the year. Figure 5 suggests that the timing of the period of adult activity may be critical in avoiding competition between adults of Carabid species in any habitat. For example, *Amara lunicollis* and *A. communis* are closely allied species with similar habits, but their adult activity maxima do not coincide. Similarly the large black Pterostichine species considered here form a series, in the order *P. madidus, P. melanarius, P. niger, A. parallelepipedus,* of increasing adult overwintering, and decreasing restriction of the period of the adult maximum. In *P. madidus* the amount of adult overwintering is least and there is a pronounced July-August adult peak, while in *Abax* there is extensive overwintering by adults of both sexes and relatively little variation in abundance between late spring and autumn. These species are all of the same order of size, and are mainly adult-overwintering and nocturnal, and there is also considerable overlap in their food and habitats; the regulation of the life history is one way in which they differ.

The timing of the annual cycles may also be important for other reasons. It may ensure that resistant stages are present at unfavourable periods of the year for there is evidence that dormant arthropods possess greater ability to withstand desiccation than active stages (Birch and Andrewartha, 1942). On the other hand Lindroth (1956b) has pointed out the necessity for the synchronisation of the annual cycle; should the breeding activity of all or part of a population become out of phase with the normal seasonal rhythm there is an increased probability of its members being wiped out by unfavourable climatic conditions. 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. *Nebria brevicollis* is the most thoroughly studied British Carabid and has a distinct adult summer diapause, and possible selective advantages associated with this can be considered.

First there is the possibility that in Britain the adult diapause in July and August is a device to survive low humidities in the summer months; the species' nocturnal woodland habits together with Tipton's (1960) work on its humidity relations, show that it is susceptible to desiccation. However, the 30 year averages of rainfall, temperature and humidity at Kew give no support to this; July and August show both higher temperatures and rainfall than either June or September and there is no fall in humidity during the hotter months. However, this factor may be important further South in Europe. It is more probable that the summer diapause delays breeding until the autumn when some environmental factor, perhaps humidity becomes suitable for the larvae, as Tipton showed that they are more susceptible to desiccation than the adults.

In addition, diapause may correlate activity in *N. brevicollis* and the availability of food. Lees (1955) cites a number of cases of phytophagous arthropods in which diapause is governed by factors similar to those which govern the growth of the food plant, thus maintaining some relation between the development of the animal and its food supply. It is difficult to relate diapause and food in *N. brevicollis* as it is a general predator on Collembola and other arthropods inhabiting litter (Davies, 1959). However, Evans (1955) gives a figure of spring and autumn peaks roughly coinciding with those of the Carabid, in the numbers of Acarina and Collembola under spruce.

Finally the diapause may synchronise breeding activity within populations. Davies (1955) and Williams (1959) found that in *N. brevicollis* breeding may extend throughout the winter; the maximum numbers of first instar larvae were recorded in mid-November, both by Williams and at the Imperial College Field Station, and the peak of spring emergence occurs approximately six months later. Occasional first instar larvae are found until the beginning of April and if they survive the summer the latest larvae may be expected to reach the adult state at least a month before the onset of the main breeding activity in October. In this way 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. More important than this, it will inhibit spring breeding by the first adult *Nebria* to appear, and thus prevent the establishment of two genetically isolated elements of the same spatial population. Lindroth (1956b) suggested that diapause had a similar synchronising effect in *Pterostichus melanarius*. Here, there is an autumn and winter diapause in the second larval instar which all individuals entered even though external conditions were varied. Thus larvae which may have hatched over a considerable period in the summer will all enter the winter in the same stage. After winter inhibition due to cold, development will be resumed in the spring by a larval population all in the same instar, so ensuring some synchronisation of adult emergence.

On the evidence available it is concluded that in Britain the diapause in *N. brevicollis* is best regarded not as a device to enable adults to survive a summer desiccation risk, but as having the effect of synchronising breeding activity, and ensuring that larvae appear when conditions are most suitable for them.

Although in most insects which have been investigated long day length is associated with growth and reproduction, de Wilde (1962) records some short day species, and noted that they tended to be autumn breeding. A number of instances are also cited in short day insects in which diapause is promoted by high temperatures. Therefore, it is possible that in *Nebria brevicollis* the summer diapause may be a response to increasing temperatures, while breeding is stimulated by short day length in the autumn.

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