Oecologia (Berl.) 23, 211–223 (1976)

Oecologia

The Influence of Weed-Cover on the Mortality Imposed on Artificial Prey by Predatory Ground Beetles in Cereal Fields

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Summary. Pitfall trapping was carried out in a field of winter wheat in the Vale of York to determine the levels of abundance of adult carabid and staphylinid beetles, (which formed the bulk of the natural predator complex) in the field. A point quadrat survey was carried out at the same time to assess the vegetation cover round each trap. Predation pressure by the beetles in the field was monitored using fruit fly (*Drosophila*) pupae as artificial prey. These artificial prey were attached to small cards inserted in the field adjacent to the pitfall traps.

The numbers of beetles caught were found to be directly related to the frequency and density of *Poa annua* L. (annual meadow grass) the only abundant non-crop plant present at the time. More beetles were caught in areas where *Poa* was abundant than where *Poa* was scarce. This was probably related to the more suitable environmental factors offered by these areas, as well as to a greater abundance of natural prey. The abundance of the wheat itself was found to be unrelated to captures.

The number of fruit fly pupae taken was shown to be related to the numbers of carabid and staphylinid beetles present, and also to the type of vegetation occuring around each card.

The implication of these results for the effects of predation on potential pest-outbreaks in the crop are discussed.

Introduction

This paper is concerned with the relationship between the weed (noncrop) vegetation present in a field of winter wheat (*Triticum*) and the predation pressure exerted by predatory ground-beetles (Carabidae and Staphylinidae) at different localities within the crop. A method of monitoring predator pressure by using artificial prey (the pupae of *Drosophila melanogaster* Meigen) is described.

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Predatory ground beetles (Carabidae and Staphilinidae) have long been considered important agents in the control of a variety of insect pests injurious to agricultural crops, and many authors have cited examples of representatives from both groups having a marked effect on the survival rate of such pests, and hence on the degree of crop damage. It has been suggested (Rivard, 1966) that the relatively high numbers of carabids in cereals render them especially useful as pest control agents. Much work has been undertaken in recent years, on crops other than cereals, to elucidate the beneficial effects of predatory beetles. Ryan (1973) has shown that the larvae of wheat bulb fly, *Leptohylemia coarctata* (Fall.), are preyed upon in the laboratory by the carabids *Agonum dorsale* (Pont.), *Loricera pilicornis* (F.), *Notiophilus biggutatus* (F.), *Clivina fossor* (L.) and *Bembidion obtusum* Ser. and staphylinids in the genus *Philonthus*. *Bembidion* spp., *Trechus quadristriatus* (Schr.), and various staphylinids [*Aleochara* spp, and *Xantholinus glabratus* (Gr.)] all take the eggs of the cabbage root fly, *Erioischia brassicae* (Bouchet) (Hughes, 1959). Coaker (1968) has shown that the number of cabbage root fly eggs in the field is inversely related to the number of carabid beetles caught in the same site, and together with *Aleochara* spp. the carabids have been shown to reduce the damage caused to the crop by this pest. Ryan and Ryan (1973) have also been able to demonstrate a similar effect with *Bembidion lampros* (Herbst.) which caused a marked reduction in the number of eggs of the root fly. Finally *Agonum dorsale*, according to Pollard (1968), climbs freely on plants, and will feed on aphids on the leaves of brussels sprouts.

The importance of this group of predators is not only confined to crops. *Pterostichus madidus* (F.) and *Tachinus rufipes* (Deg.), a carabid and a staphylinid respectively, are important predators of the broom weevil *Sitona regensteinensis* (Hbst.) (Danthanorayama, 1969), whilst *Pterostichus melanarius* (Ill.) *P. madidus, Abax parrallelopipedus* Pill & Mitt.) and *Philonthus* spp. feed on the pupae of the winter moth [*Operophtera brumata* (L.)], with important consequences for the population dynamics of this organism (Frank, 1967; East, 1974).

Not all species of carabid are entirely carnivorous. For example *Pterostichus melanarius* and *P. madidus* are both known to damage stawberries (Luff, 1974). However many of the species which take plant material are also known to be carnivorous (Sunderland, 1975). In general it is reasonable to assume that virtually all the carabids and staphylinids mentioned in the present investigation [with the exception of *Amara* spp. which are generally herbivorous (Lindroth, 1974; M.L. Luff, pers. comm.)] are predatory, although some of the species are not entirely carnivorous at all times.

The present study is concerned entirely with adult beetles. A large number of species of both carabids and staphylinids occur in cereal fields in Yorkshire, including all the species listed in the discussion above. A detailed analysis of this assemblage of predators will be made in a later publication. The present work directs itself to the question: given that ground-beetles are potentially important as predators within a crop, what features of the cereal-ecosystem serve to enhance or hinder the predator-pressure which they exert?

In seeking to answer this question, we considered a number of hypotheses. One obvious possibility was that the quantity and variety of weeds growing within the crop would be important. As long ago as 1961, Pimentel showed that plant species diversity played an important role in preventing insect population outbreaks on *Brassica* plants, whilst Rivard (1966) has suggested that the weedy vegetation associated with cereals may influence the extent to which carabids are controlling agents for pest species. Potts and Vickerman (1975) have shown that cereal fields with a high floral (i.e. weed) diversity have a much greater diversity of arthropod species than 'clean' fields. Other important links which they establish are a higher proportion of predatory arthropods in faunally diverse fields and larger populations of apterous aphids (potential or actual pests) in fields with a low faunal diversity.

Problems of this type can obviously be investigated on at least two, ultimately related, levels; namely gross (between field) comparisons (Potts and Vickerman, 1975) and on a smaller scale, comparisons between different localities within one field. The present work, which forms part of an investigation concerned with both within and between field comparisons, focuses on the small-scale effects of weed-cover within one field.

Methods

Our study area was a 10 a (4 ha) field of winter wheat in the Vale of York (Map Reference SE 551466). Sampling was carried out over the 2-week period 17 June–1 July 1975, the beetle populations being monitored using pitfall traps. Although these have inherent disadvantages for certain types of investigation (Mitchell, 1963; Greenslade, 1964a; Luff, 1975), we considered them to be the most useful method of sampling for the purpose of this study. The traps consisted of plastic coffee cups, 9 cm deep by 7 cm diameter at the top, sunk in the soil with their rims flush with the surface. In each cup was placed approximately 50 ml of killing fluid (prepared in bulk from 30 ml concentrated formaldehyde solution and 250 ml of absolute alcohol made up to 2 l with water). A few drops of detergent were added to ensure that animals caught sank to the bottom of the traps and so reduced escapes and predation on the traps to a minimum. The quantity and concentration of the killing fluid were kept constant throughout the experiment to reduce errors occurring due to the attractive properties of the fluid to certain beetle species (Luff, 1968). The traps were left in the ground for 14 days. After this time, the traps were removed and the contents sorted into species and counted in the laboratory.

Two sets of traps were used, laid out as shown in Figure 1. In the first, 30 traps were laid down in a transect approximately 10 m apart across the field; each trap in the transect was placed in an area of similar vegetation (crop and weeds), assessed by eye. In the second, the traps were put down in a group toward the centre of the field, each being located in an area with a different amount of plant cover. The areas selected were in the centre of the field to reduce any errors which might have resulted from the field edges having a different beetle fauna from that in the body of the field (an 'edge effect'; see "Results"). When this second group of traps were collected, a survey of the vegetation surrounding each one was carried out using a point quadrat system. The apparatus consisted of a 1 m square quadrat with an evenly spaced wire lattice strung across it, resulting in a grid of 49 intersections which were used as reference points in the survey. The quadrat was supported on bamboo legs 1 m high to avoid damage to the wheat. In each case the central intersection of the quadrat was placed directly over the pitfall trap, so that the same area around each trap was sampled at each site. A thin (2 mm diam.) metal rod was let down vertically from each intersection to the ground below, and any plant (both weeds as well as the crop itself) touched by the vertical needle was recorded. When totalled up for all the intersections, this gave an estimate of the frequency of each plant-species. The number of shoots (leaves) of each species touching the needle was also noted, giving a density measurement as well. Hence measurements for plant frequency and density (i.e. presence and absence data, and the thickness of ground cover) were obtained for a square meter around each pitfall trap. Note that since

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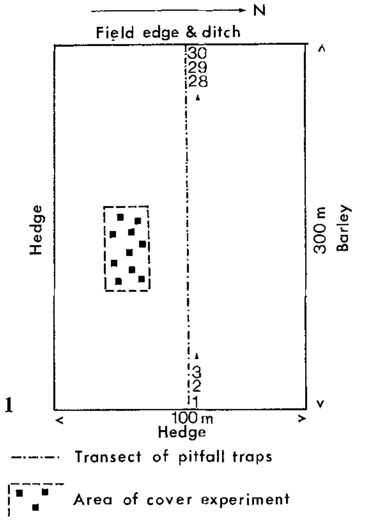

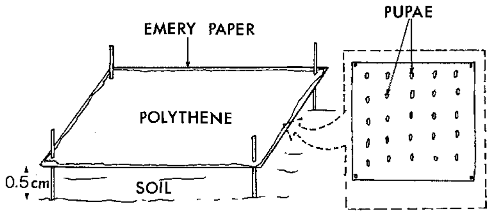

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Fig. 1. Map of the study field showing the relative positions of the two sets of pitfall traps. Each trap in the group in the centre of the field had a card of *Drosophila* pupae closely associated with it, as had the last 10 traps in the transect. Distances are only approximate

Fig. 2. Diagram of cards used to expose *Drosophila* pupae in field

we only required a measure of vegetation structure that allowed relative comparisons to be made between different areas, all involving the same species of plants, the well known problems that occur because the pin is not a true point (e.g. Greig-Smith, 1964, p. 43) are not important in the present context.

Predation pressure at various points in the field was assessed using *Drosophila* pupae. The pupae were killed by deep freezing to prevent emergence during the experiment, and were then attached to 10 cm^2 cards of emery paper, on the rough side, using a small regularly sized spot of flour paste. The pupae were laid on the cards, 25 to each, in a regular 5×5 grid. The cards were covered on the smooth upper side with polythene for weather protection, and then placed in the field with wooden supports at each corner, 0.5 cm above the soil surface, with the pupae facing downwards (Fig. 2). Each card was closely associated with a pitfall trap. They were left for 24h, after which time they were collected, the number of pupae attacked and removed counted, and a fresh card inserted at the same spot. This procedure continued for 4 days. Pitfall trapping therefore continued for 10 days after removal of the last cards. (The different periods of time used to measure predation on the cards and to monitor beetle numbers were not the result of any subtle biological considerations. The pitfall trapping formed part of a routine monitoring programme in a large number of other fields, using a 14-day trap-run. Four days were as long as our limited supply of *Drosophila* pupae lasted.)

Attacked pupae were readily recognised as either opened puparia, remaining fragments, or identations left in the flour paste where the pupae had been removed. In the laboratory *Pterostichus melanarius, Nebria brevicollis* (F.), *Agonum dorsale* and *Philonthus fuscipennis* Man., along with other smaller beetles (e.g. *Bembidion* spp.), have all been observed to remove *Drosophila* pupae from the cards very readily, leaving the same characteristic traces that were observable in the field. Under controlled conditions of varying moisture regimes, the pupae remain stuck to the cards for well over the 24-h period that they remain in the field, even when soaking wet; some external agency is needed to dislodge them. A further check which reinforces the likelihood that ground-living predators were the agencies of removal is that in the field pupae on upturned cards were not removed. The actual animals involved in pupal removal in the field were obviously difficult to specify with absolute certainty. However, the characteristic appearance of the predated pupae, and the fact that pitfall trapping and general collecting in the field indicated that only certain groups were available to carry out predation (of which the carabids and staphylinids were by far the most common), suggests that other agents were unimportant. The weather throughout this experiment was hot, dry and settled, considerably reducing the activity of other possible (but unlikely) predators such as slugs.

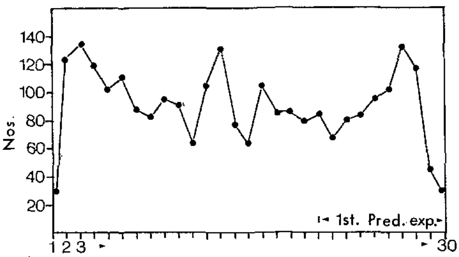
Results

Weeds and Predator Numbers

Table 1 summarises the data on the adult carabid and staphylinid beetles caught in the first set of pitfall traps (the transect) over the 14-day trapping period. They constitute a typical sample of the ground beetles found in early summer in winter wheat in Yorkshire (Speight, unpublished). A small 'edge effect' is observed, where traps at the field edges yield smaller catches than those in the body of the field (Fig. 3). This is a normal feature of the distribution

Table 1. Total carabids and staphylinids caught in the first set of pitfall traps (30 traps laid out in a transect across the field). 17 June to 1 July 1975

Species	Total caught
Carabidae	
Abax parallelopipedus	1
Agonum dorsale	179
(*Amara plebeja*) (Gyll.) non-predatory (see text)	144
(*A. similata*) (Gyll.) non-predatory (see text)	2
Asaphidion flavipes	1
Bembidion lampros	1
Clivina fossor	5
Harpalus aeneus (F.)	2
Harpalus rufipes	9
Loricera pilicornis	25
Nebria brevicollis	14
Notiophilus biggutatus	1
Pterostichus madidus	7
P. melanarius	1,456
P. nigra (Schall.)	12
P. strenuus (P.)	2
Trechus quadristriatus	2
Staphylinidae	
Aleocharini	205
Conosoma spp.	2
Oxytelus sculpturatus (Grav.)	2
Philonthus fuscipennis (Mann.)	466
Philonthus spp.	2
Tachinus rufipes	75
Tachyporus chrysomelinus (L.)	5
T. hypnorum (F.)	73
T. obtusus (L.)	2



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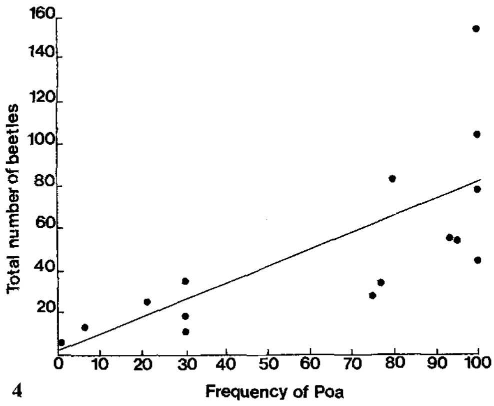

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Fig. 3. Total numbers of ground beetles caught per trap over 14 days in the transect of pitfall traps laid out in areas of similar vegetation cover. The last 10 traps had pupal-cards associated with them, as indicated

Fig. 4. Total numbers of ground beetles caught per trap per 14 days as a function of the percentage frequency of weeds (*Poa annua*) in 1 m^2 round each trap (second set of traps, laid out as a group in the centre of the field). $Y = 1.12 + 0.77\, X$; $r = 0.72$; $0.01 > P > 0.001$

of ground beetles in cereal fields at this season of the year will be discussed further in a later publication.

The beetles caught in the second set of traps placed as a group in the middle of the field in different vegetation regimes were, as expected, virtually identical in their species composition. Table 2 shows the numbers and Table 3 gives the results of the point quadrat survey round each trap. It will be clear from Table 3 that the only species of plant present in any quantity, besides wheat, was *Poa annua* L., the annual meadow grass, and our analysis has therefore been confined to the effects of this species and that of the crop itself. *Poa annua* has a decumbent, creeping growth form, and tends to form a mat of vegetation at ground level within the crop.

The total numbers of predators captured in the second group of traps was significantly related both to the percentage frequency of *Poa*, ($0.01 > P > 0.001$) and to the number of shoots of the grass ($0.001 > P$) (Figs. 4 and 5). A more detailed analysis of the combined effects of frequency and density of *Poa* on captures, for example by multiple regression, was not possible because of the high degree of correlation between these two measures of weed abundance (Fig. 6). The effects of the crop itself on the catch of the predatory beetles was insignificant (Table 4). This is not surprising in view of the very narrow ranges of cover and density shown by the crop (farmers sow seeds to achieve great uniformity in the distribution of their plants), and the fact that the vertical stalks carry much of the cover above the zone of activity of the beetles.

Table 2. Pitfall captures of carabids and staphylinids from the second set of traps laid out in a group in areas of differing plant cover

Species	Numbers caught														
	Trap no.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Carabidae															
Agonum dorsale	2	1	1	1	—	3	2	—	1	7	1	—	1	—	—
Amara plebeja	2	2	1	7	11	38	13	1	12	13	4	3	1	2	11
Bembidion quadrimaculatum (L.)	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Clivina fossor	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
Harpalus aeneus	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
H. rufipes	—	1	—	—	3	1	1	—	1	3	—	1	—	—	6
Loricera pilicornis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Notiophilus biggutatus	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Pterostichus melanarius	18	17	27	15	65	33	16	22	36	75	16	4	10	7	127
P. nigra	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Staphylinidae															
Aleocharini	—	3	10	3	—	—	—	1	—	—	—	1	—	—	14
Philonthus fuscipennis	—	—	—	—	1	1	—	—	—	6	—	—	—	—	—
Philonthus spp.	—	—	6	13	—	—	—	—	—	—	—	—	—	—	6
Tachinus rufipes	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—
Tachyporus hypnorum	4	4	—	3	—	3	—	—	3	—	—	3	—	—	—
T. obtusus	—	3	—	1	—	—	—	—	—	1	1	—	—	—	—

Table 3. Vegetation data from point quadrat sampling (1 m^2 around each pitfall trap in the second set of traps). *Poa* = *Poa annua*; *P. avic.* = *Polygonum aviculare* L.; *T.* = *Tripleurospermum maritimum* (L.)

Trap no.	Percentage frequency				Density			
	Wheat	*Poa*	*P. avic.*	*T.*	Wheat	*Poa*	*P. avic.*	*T.*
1	96	76	—	—	168	121	—	—
2	86	78	—	—	137	125	—	—
3	90	94	—	—	144	148	—	—
4	86	96	—	—	162	143	—	—
5	16	78	22	28	10	195	15	23
6	28	96	16	20	28	174	9	19
7	26	30	—	—	20	36	—	—
8	34	22	—	—	25	23	—	—
9	6	94	2	—	3	243	1	—
10	16	100	—	—	9	250	—	—
11	2	30	14	—	1	126	7	—
12	2	30	—	—	1	42	—	—
13	—	6	—	—	—	3	—	—
14	—	—	—	—	—	—	—	—
15	70	100	—	24	88	440	—	34

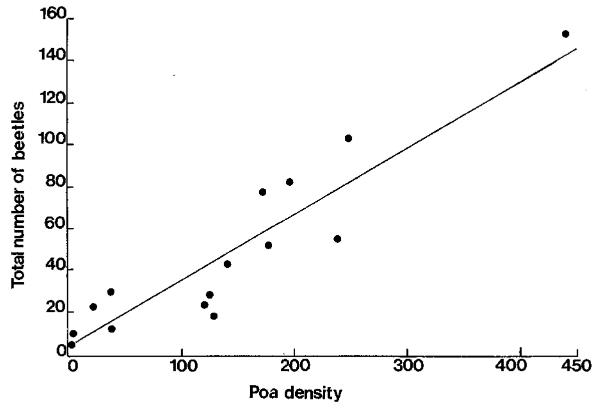
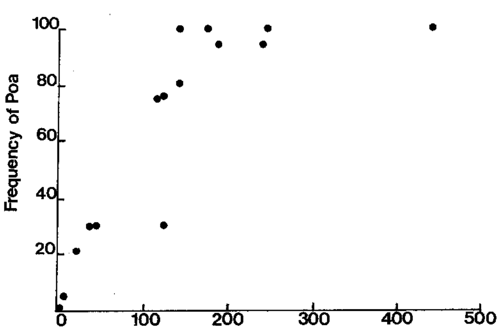


Fig. 5. Total number of ground beetles caught per trap per 14 days as a function of the density of *Poa annua* in 1 m^2 round each trap (second set of traps, laid out as a group in the centre of the field). $Y=4.70+0.32\,X$; $r=0.92$; $0.001>P$



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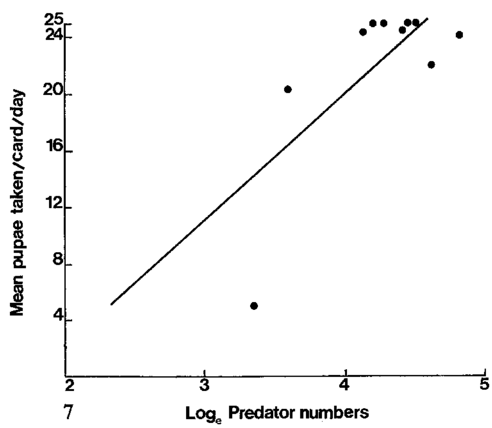

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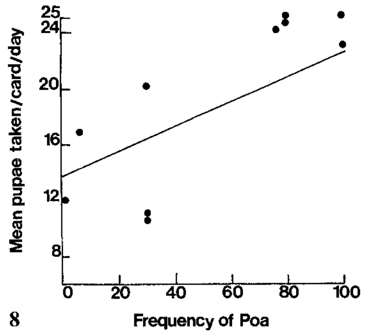
Fig. 6. Relationship between frequency and density of *Poa annua* in 1 m^2 quadrats (data as in Table 3) (regression not calculated)

Fig. 7. Mean number of pupae removed per card over 4 days, as a function of the number of predatory beetles (all ground beetles excluding *Amara*) caught in the transect of traps in areas of similar vegetation. $Y=-20.16+9.98X$; $r=0.73$; $0.02>P>0.01$

Table 4. Data from multiple regression of wheat density and *Poa* density on pitfall trap captures in the second set of traps

Regression eq. $Y=0.329\,X_1-0.083\,X_2+7.60$		
F value for mult. reg.	36.08	$0.005>P>0.001$
F value for *Poa* alone	71.59	$0.005>P>0.001$
F value for wheat alone	1.45	N.S.

Fraction of variance explained by multiple regression 0.84.
Poa density accounted for 98% of the variance explained.



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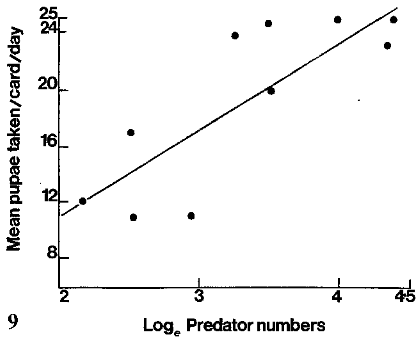

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Fig. 8. Mean number of pupae taken per card over 4 days, as a function of the frequency of *Poa annua* in a 1 m^2 round each card (second set of traps, laid out as a group in the centre of the field in areas of variable vegetation cover). $Y=12.28+0.13\,X$; $r=0.83$; $0.01>P>0.001$

Fig. 9. Mean number of pupae taken per card over 4 days, as a function of the number of predatory beetles (all ground beetles excluding *Amara*) caught in the second set of pitfall traps positioned in areas of variable vegetation cover in the centre of the field. $Y=-2.04+6.92X$; $r=0.87$; $0.01>P>0.001$

Weeds, Beetles and Predation Pressure

Figure 7 shows the mean numbers of pupae attacked from four replicate cards set out adjacent to the transect of pitfall traps across the field in areas of similar plant cover. Although the relationship between the log. of predator numbers and predation pressure is statistically significant ($0.02>P>0.01$), it hinges almost entirely on the two traps and the associated cards situated at the end of the transect. The field as a whole was fairly 'weedy', so that the line of pitfall traps tended to be positioned in areas of weed cover that visually at least, fell towards the top end of the range encompassed by the second set of traps. In consequence beetle numbers were high and the cards in the transect had most, or all, their pupae removed each night.

Predation measurements carried out in areas of different plant cover, with the second set of traps, produced rather clearer results. We now have highly significant relationships between the frequency of *Poa* and the 'mortality' imposed by predators on the pupae ($0.01>P>0.001$) (Fig. 8), and as expected, between predator numbers and pupal 'mortality' ($0.01>P>0.001$) (Fig. 9). As with the first line of traps, the number of pupae removed per night when predators were common tended to approach the maximum possible number (25); this almost certainly explains why pupal mortality was significantly linearly related to the log. of predator numbers and not to their untransformed abundance.

Note that the regression shown in Figures 7 and 9 exclude the non-predatory carabids in the genus *Amara*. Examination of Tables 1 and 2 will show that these constituted a significant part of the total catches of ground beetles. If the individuals of this non-predatory genus are included in the total numbers of beetles caught, the relationship shown in Figure 9, for example, is weakened substantially ($r=0.65$ instead of 0.87), which lends support to our argument that it is the predatory beetles that are removing the pupae.

Discussion

Within one field, areas of high weed cover have more predatory ground beetles, and artificial prey suffer significantly greater 'mortality' than areas with few weeds. Over the field as a whole, comparing areas of similar vegetation type, only the edges have few beetles, and low levels of predation.

The decline in the numbers of carabids and staphylinids caught at the field edges in the first line of traps is probably the result of three factors. First the edge of our study field consisted of a thin (1 m wide) strip of dense tufts of *Agrostis stolonifera* L., nettles (*Urtica dioica* L.) and brambles (*Rubus*) followed by a wide deep ditch, a thin line of willows (*Salix*), and then another cultivated field. Woodland species of beetle, which, when present, can swell the populations at field edges (Rivard, 1966), were not evidence because of the lack of suitable habitats. Second, it is very likely that the resistance to movement of ground beetles afforded by the strip of dense vegetation at the edge was high, hence further reducing the movement of beetles into the field (Greenslade, 1964b). Furthermore, it has been shown by Pollard (1968) that certain species of carabid, e.g. *Pterostichus melanarius*, *P. madidus*, *Loricera pilicornis* and *Harpalus rufipes* (Deg.) [all of which are commonly caught in winter wheat (Tables 1 and 2)], have no apparent association with hedges surrounding arable land, which could help to account for lower catches of these beetles at the field edge.

A reduction in the effectiveness of this particular group of predators at the field edge appears to run counter to the popular view that such habitats provide a reservoir for predators and thus to enhance the regulation of crop pests.

Pitfall captures in the body of the field were clearly associated with the frequency and abundance of the ground covering weeds (*Poa*), but not with the vertically growing wheat shoots. In general, we might also expect the *diversity* of the weed species present to be of importance (Murdoch et al., 1972; Pimentel, 1960; Speight, unpublished) but since our study area was dominated almost entirely by *Poa* to the virtual exclusion of all other weed-species, the diversity of the weed cover could be eliminated as an important variable in the present investigation.

The relationship between pitfall trap catches, and hence beetle activity, and the frequency and abundance of *Poa* is probably complex, but it is likely that the role that the weeds play in protecting the predators from extremes of climate, i.e. insolation during the day, and desiccation both during the day and at night is important. Rivard (1966) found higher catches of carabids in area of higher humidity, and Thiele (1964) considers that humidity is the key to the abundance of the majority of carabids, and that microclimate in the crop is very important. It is reasonable to suggest that the relative humidity under a fairly dense carpet of groundlying grass shoots, as in *Poa*, is greater than on bare soil, especially in warm weather, and at night after a hot day.

As well as microclimatic considerations, it is also possible that there is an indirect effect operating via the abundance of natural prey, which may be commoner in the denser patches of *Poa*. Thus Potts and Vickerman (1975) found a positive relationship between the numbers of predatory Coleoptera in cereal fields and the abundance of macroscopical Isotomidae (Collembola). Whether prey numbers were themselves related to weed abundance was not reported. Finally, as we have already noted, Greenslade (1964b) found the highest catches of carabids, in particular *Nebria bevicollis*, in litter, where the litter offered the least resistance to carabid movement, and we have suggested that this may have contributed to the 'edge effect'. In contrast, the positive relationship between *Poa* density and beetle abundance in the body of the field presumably reflects the fact that even the highest weed densities were still below those at which carabids and staphylinids experience any marked restrictions on their movement.

Obviously, we are concerned here with the effects of the total predatory beetle complex. Cetain individual species of carabid seek out bare ground, e.g. *Bembidion lampros*, which occurs in the study area (Table 1) and which is known to be an important predator of cabbage root-fly eggs (Ryan and Ryan, 1973). Numbers in this species are inversely correlated with the amount of plant cover (Mitchell, 1963). The results obtained in the present study suggest that this response is not typical of the predatory ground beetle complex of the field taken as a whole.

Although not important in the present investigation the effect of the crop itself can not be entirely ignored, since some degree of protection will be afforded to the ground below (see Monteith, 1973, p. 204), and this, although perhaps rather insignificant in the case of wheat, will be quite marked for such crops as barley, where the individual plants are much closer together. Pitfall trapping carried out in spring barley has yielded very high carabid and staphylinid numbers, comparable with those from winter wheat containing a high density of weeds (Speight, unpublished).

The rather high variance associated with the pupal predation data probably reflects the large element of chance involved in the predators locating and eating the prey offered to them in the small, descrete groups presented by the individual cards. Mitchell (1963) has pointed out that both *Bembidion lampros* and *Trechus quadristriatus,* both possible predators of pupae in the field, change their behaviour on finding cabbage root-fly eggs. Characteristic of a large number of predatory insects (Hassell and May, 1974), they make slow, tight turns for 10–15 s after eating one egg, presumably to seek out other prey in the vicinity. If predators, coming randomly upon cards of pupae laid out in the field, follow this behaviour pattern, then large numbers of pupae could be removed by one beetle. Despite such effects the results are unequivocal, and suggest that the use of artificial prey, of the form used in this study, is a very good means of monitoring the predation pressure exerted by predatory ground beetles.

Our study has a number of obvious, but unproven, implications. Within one field, an increase in the quantity of weeds was correlated both with an increase in the abundance of predatory ground beetles, and with an increase in the disappearance of artificial prey. It is tempting to extrapolate these results to a between field comparison and suggest that 'clean' fields will have fewer predatory ground beetles than weedy fields, and in consequence experience lower levels of predation, with the result that outbreaks of certain types of potential crop pests are more likely in weed-free fields. The long series of unproven and hidden assumptions in this argument makes it particularly dangerous. Between field comparisons involve other important factors, for example differences in field-size, and crop husbandry which may markedly influence the predatory beetle complex (Potts and Vickman, 1975; Speight, unpublished) whilst the demonstration that a particular type of prey organism experiences a high-level of predator attack by no means ensures that the prey will persist at a low and stable level of abundance (Beddington et al., 1975; Watt, 1965). The results obtained in the present study merely form one small part of the highly complex, but important jigsaw puzzle of ever-changing relationships that determine the levels of abundance of prey and predators in cereal ecosystems.

Acknowledgements. This work was carried out during the tenure by M.R.S. of a research studentship from the Ministry of Agriculture, Fisheries and Food, and forms part of a study to be presented to the University of York for the degree of D. Phil. The authors wish to thank the Principal and staff of Askham Bryan College of Agriculture, Askham Bryan, York, for permission to sample in their cereal fields. Professor Mark Williamson and David Thompson made a number of very helpful suggestions on the first draft of this paper.

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Received December 27, 1975