

Activity and satiation state in *Pterostichus melanarius*: an experiment in different agricultural habitats

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Abstract. 1. A capture–recapture experiment was conducted to examine the effects of satiation state on the activity and foraging efficiency of the carabid beetle *Pterostichus melanarius* Ill., in four different habitats (a hedge, a transition zone between the hedge and the adjacent wheat crop, the margin of the wheat crop, and the centre of the wheat crop) in an agricultural ecosystem in France.

2. Prey biomass and density decreased from the centre of the hedge to the crop margin and to the centre of the crop, where prey density was low but prey biomass was moderate. Starved and satiated beetles were released in circular enclosures and recaptured using pitfall traps for 6 days.

3. Immediately after release, starved *P. melanarius* were significantly more active than satiated beetles, but this difference disappeared after the first day. At each recapture date, starved individuals had gained weight whereas satiated individuals had lost weight. The analysis of activity and weight variation at the end of the first day indicated that the centre of the crop seemed to be the most favourable habitat for starved individuals to find food rapidly, whereas the behaviour of satiated individuals was identical in all habitats.

4. This experiment shows that habitat use of *P. melanarius* is flexible. The results are discussed in the context of the classical view of foraging behaviour in carabid beetles. The activity and foraging efficiency in *P. melanarius* in different habitats can be explained as the result of the interaction between individual satiation state, prey availability in the habitat, and particular preferences of the species.

Key words. Capture–recapture, field margin habitats, foraging activity, *Pterostichus melanarius*.

Introduction

Undisturbed field margins are associated with elevated populations of predatory arthropods in agro-ecosystems (Nentwig, 1988; Desender *et al.*, 1989; Lys, 1992, 1994; Thomas *et al.*, 1992; Zangger, 1994). Previous work in a region of intensive agriculture (Fournier & Loreau, 1999) showed that the diversity of ground beetles (Coleoptera, Carabidae) declined significantly with increasing distance from a recently established hedge towards the field centre. The various species had different distribution patterns, however, indicating different habitat choice strategies.

Thiele (1977) argued that only abiotic factors determined carabid activity between and within habitats, however biotic processes (such as foraging, reproduction, predation pressure, overwintering) are also known to be important (Evans, 1990; Lövei & Sunderland, 1996). In particular, some authors (e.g. White, 1978) have stressed the importance of finding sufficient suitable food, however the exact determinants of insect foraging strategies in different habitats are poorly understood. This knowledge is relevant to the present development of integrated agricultural systems because foraging strategies affect how diversity may be maintained by habitat heterogeneity. For example, at the study site, recent establishment of hedges at field margins has created a mosaic of new habitats. Understanding how foraging strategies of predatory insects such as ground beetles are modified by habitat structure may be of great interest for management of pests and, ultimately, for their biological control.

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Foraging activity of carabids is mostly motivated by hunger (Grüm, 1971a,b; Baars, 1979; Mols, 1982, 1987; den Boer, 1986) and displacements are modified by prey intake (Mols, 1982, 1987; den Boer, 1986). Just after prey is eaten, tortuous walk is adopted, followed by random walk, then directed walk if no prey is found. When the insect is totally satiated, however, it remains inactive during the beginning of the digestion process. Consequently, this hypothesis recognises two main satiation states (starved and satiated), and assumes that starved individuals are more active than satiated individuals, and that this activity is due to foraging. This hypothesis has rarely been tested in natural conditions.

Habitat features also play a role. First, prey availability (both prey densities and prey diversity) influences a beetle's satiation state and hence its activity directly. Second, microclimatic conditions or the physical structure of vegetation also influence the beetle's ability to move in the habitat or to be sensitive to prey stimuli (Cárcamo & Spence, 1994, and reference therein). These abiotic factors are directly related to the beetle's habitat preferences.

A capture–recapture experiment was performed at a local scale, in adjacent habitats established at a field margin: a hedge, a transition zone, and the field itself. The experiment aimed to test two hypotheses: Is there a relationship between foraging activity and satiation state (gut contents)? Is this relationship modified as the habitat changes, especially when prey availability varies among habitats?

Materials and methods

Study area

The study area was situated on an experimental farm in the intensively cultivated French region of Beauce (48°22'N, 1°45'W). Hedges were planted during winter 1994–1995, as described in detail by Fournier and Loreau (1999). They were composed of two elements: two rows of shrubs 200 m long and 6 m wide (hedges *sensu stricto*), and a mixed crop of fodders (oats, cabbages, buckwheat) 100 m long inserted between the two rows of shrubs. This composite line (total length 500 m) was separated from the adjacent crop (winter wheat in 1997) by a 9-m wide zone planted with the same mixed crop. Four habitats thus followed each other along a 120-m long gradient: hedge *sensu stricto*; mixed crop; the first 10 m of winter wheat crop (hereafter called *crop margin*); and the centre of winter wheat crop, 100 m from the crop margin.

The hedge cannot be considered a closed habitat because its maximum height did not exceed 2 m, however the physical structure of the vegetation was more complex in the hedge than in the mixed crop, and more complex in the mixed crop than in the wheat crop. There was also a gradient of disturbance among these habitats: the hedge was undisturbed, the mixed crop little disturbed, whereas the margin and the centre of the wheat crop experienced

frequent disturbances associated with prevailing agricultural practices. These gradients had two potential consequences. First, they generated a gradual change in the presence of refuge sites for carabid beetles: because of its more complex vegetation structure and the absence of disturbance, the hedge was likely to offer more refuge opportunities. Second, the hedge was likely to offer a greater prey diversity (Lewis, 1969; Fournier & Loreau, 1999).

Measurement of prey availability

Two methods were employed to measure prey availability in the various habitats. First, captures made using pitfall traps installed at various distances from the hedge during April–July 1996 (adjacent crop was spring barley) were analysed. Traps were situated at the following distances from the hedge: 0 m (i.e. centre of the hedge; 15 traps), 10 m (i.e. limit between the mixed crop and the adjacent barley crop; four traps), 20 m (i.e. in the first 10 m of the adjacent barley crop, thus equivalent to the present wheat crop margin; four traps), and 110 m (i.e. equivalent to the present wheat crop centre; four traps). Thus, the mixed crop habitat was not sampled by this method.

Insects were identified to family level, except for Collembola, which were numerous in all traps and excluded. Other groups of invertebrates (araneids, annelids, molluscs, myriapods) were also found but these were not counted. Because pitfall traps give a biased view of prey density (the various types of prey are not equally represented in samples because of differences in their mobility and ability to escape from traps), this method was essentially used to illustrate differences in prey diversity among habitats.

A second method consisted of formaldehyde extractions from quadrats, by watering a quadrat of soil (25 × 25 cm) with a solution of formaldehyde (dilution 0.04%) twice during a 20-min period (eight quadrats in each habitat in July 1997). Animals irritated by formaldehyde tried to escape from the quadrat or became very active at the soil surface. This method is usually employed to sample earthworms but allows sampling of other invertebrates (Guillemain *et al.*, 1997), however some kinds of organisms, such as Collembola, are difficult to catch by hand. The catch was differentiated into four groups: three groups for annelids based on their usual microhabitats (epigeic, i.e. soil-living; anecic, i.e. intermediate depth-living; endogeic, i.e. depth-living) and other kinds of prey. In the four classes, each item (except again Collembola) was counted and weighed to the nearest milligram.

Enclosures

Two 5-m diameter circular enclosures (replicates) were installed 500 m apart in each of the four habitats. These enclosures were made of plastic sheets 50 cm high, maintained vertically with stakes, and buried in the soil up to a depth of 10 cm. In each enclosure, eight pitfall traps were spaced evenly along the interior wall. Because this experimental design is

limited to two replications and to adjacent hedges, results concern local effects.

Species studied

Pterostichus melanarius Ill. is a nocturnal (Greenslade, 1965; Lindroth, 1992), autumn breeding carabid (Lindroth, 1974, 1992; Thiele, 1977); individuals range between 12 and 18 mm in length (Jeannel, 1941, 1942; Lindroth, 1974, 1992). It is eurytopic but mainly prefers open habitats and is rather favoured by agriculture (Desender & Alderweireldt, 1988). June is a period of great activity for this species, corresponding to the emergence of teneral adults that are active for foraging (Fadl *et al.*, 1996); reproduction occurs in August–September. As in many carabids, this species has a very unspecific diet (Pollet & Desender, 1985), including numerous items of crop pests (Sunderland, 1975; Sunderland & Vickerman, 1980; Pollet & Desender, 1987). This predator is apparently able to adapt to local and temporal variations in prey availability in pasture systems, and forages mainly on the most available prey (Pollet & Desender, 1986, 1987), indicating that *P. melanarius* is an opportunistic predator. Symondson (1997, pers. comm.) reported similar results for *P. melanarius* preying on slugs when these are the dominant prey. Several authors (e.g. Duelli & Obrist, 1995) have shown that *P. melanarius* is abundant in cereals, grasslands, and heathlands but not in woodlands and hedgerows. This was not the case in this study: in a previous survey (Fournier & Loreau, 1999), *P. melanarius* was found to be the most abundant species in the whole study area. According to its spatial distribution, *P. melanarius* was classified as hedge indifferent exhibiting a slight preference for the crop. This may be due to the fact that hedges were only 2 years old at the time of the study.

Manipulation of satiation state

The beetles were collected in the field from 20 May to 10 June 1997, and held in individual plastic boxes with a thin layer of soil and filter paper, which was moistened daily. They were brought back into a hangar close to the field, maintained at ambient temperature, and were fed every 4 days with earthworms. When a sufficient number was available, all beetles were starved for 6 days, with *ad libitum* access to water. After starvation, they were weighed (to the nearest milligram) to determine the basal weight of individual *i* after 6 days of starvation ($W_{B,i}$). Beetles were then separated into two satiation-state groups: starved and satiated. Satiated individuals were fed with earthworms *ad libitum* for 24 h, while starved individuals were not fed. The beetles were marked differently on the elytra according to their satiation-state group, using a microdrill to make small permanent nicks in the insect's cuticle that do not affect insect survival and behaviour (Loreau, 1984). After 1 day, satiated insects were reweighed. The initial weight of individual *i* of satiation-state group *g* was termed $W_{0,g,i}$. Starved individuals were not weighed again before release, so $W_{0,ST,i} = W_{B,ST,i}$.

Pterostichus melanarius is not stringent as regards rearing conditions (Tomlin, 1975; Ericson, 1977). Samples were not checked for homogeneity with respect to age class and sex, which could influence food intake and activity (Makowski & Szyszko, 1986), but the experiment was not performed during the reproductive period of *P. melanarius*, so that differences between sexes in activity and food intake were probably negligible.

Measurement of activity level and body weight variation

The experiment was performed with 128 *P. melanarius* in the starved group and 130 in the satiated group. In each enclosure, 16 (± 1) starved and satiated individuals were released on day 0. Traps were then checked every day for 6 days and the mark of each recaptured individual *j* was determined under a binocular lens. Each beetle was weighed (to the nearest milligram) to determine the body weight at recapture of individual *j*, belonging to satiation-state group *g*, and recaptured in enclosure *k* ($W_{C,j,g,k}$). After recapture, the beetle was removed from the experiment (i.e. released outside the enclosure). The number of individuals recaptured daily in each enclosure was taken as an estimate of total activity.

It was not possible to follow the variation in weight of individual beetles because they did not carry individual marks. The mean initial weight of each satiation-state group *g* in each enclosure *k*, $\bar{W}_{0,g,k}$, was thus calculated and was used as the initial weight for group *g* in enclosure *k*. The ratio between the recapture weight of individual *j* and the mean initial weight of the group in each enclosure WR_j , was calculated as $WR_j = W_{C,j,g,k} / \bar{W}_{0,g,k}$. This variable was used to study the changes in weight between release and recapture (the length of this period may be 1–6 days).

Statistical analyses were performed with the SAS software (SAS, 1989). Procedure CATMOD was used to analyse contingency tables, and procedure GLM with nested models was used to analyse variable WR_j (with replicate effect nested into habitat effect).

Results

Prey availability

Numbers of potential prey individuals captured by pitfall traps were sufficient for seven families (Tetanoceridae, Staphylinidae, Formicidae, Jassidae, Bibionidae, Sciaridae, Scathophagidae) to test for differences in frequency distributions among habitats. The less abundant 32 families were grouped into four categories (other Coleoptera, other Diptera, other Hymenoptera, other Hemiptera + Diplura) for analysis. Distribution of captures across these 11 categories differed significantly among habitats ($\chi^2 = 679$, d.f. = 30, $P < 0.001$). Prey richness decreased with increasing distance from the hedge; prey diversity measured using the Shannon's index was high in the hedge and low but stable in the other habitats (Fig. 1). Insect families were also grouped according to their

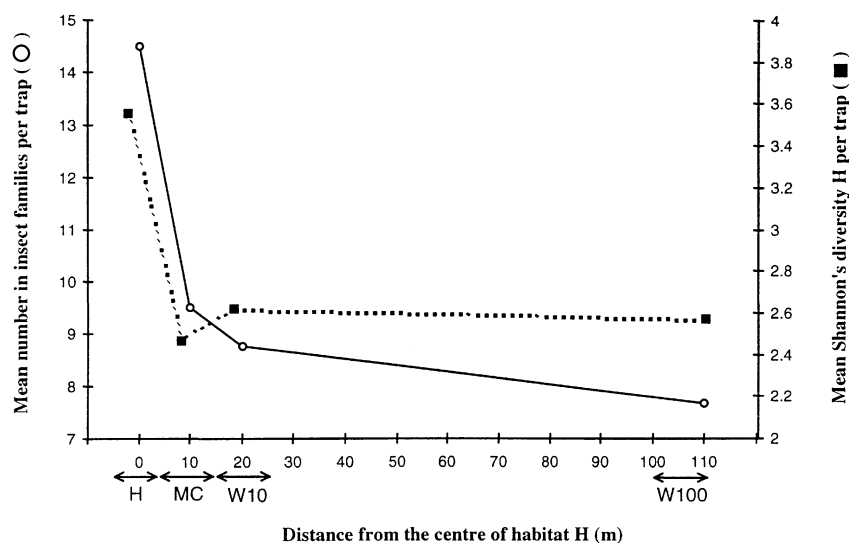


Fig. 1. Number of insect families (○) and Shannon's diversity index (■) in pitfall traps (means per trap) as a function of distance from the centre of the hedge (sampling in spring 1996). Carabidae and Collembola are not included. H: hedge, MC: mixed crop, W10: wheat crop margin, W100: wheat crop centre.

diet to test for differences in trophic structure among habitats (those known to be xylophagous or saprophagous, and unknown diets, were excluded from the test). Polyphagous and parasitic insects were distributed evenly, phytophagous insects were more abundant in the crop, and predatory insects were more abundant in the hedge (test on the whole contingency table: $\chi^2 = 432$, d.f. = 9, $P < 0.001$).

Formaldehyde extraction in quadrats is a better method to test for differences in prey density and biomass, although it can be used for only a restricted range of prey items. Extractions varied significantly among habitats with respect to total prey density measured as the total number of prey caught ($\chi^2 = 96.2$, d.f. = 3, $P < 0.001$). Total prey biomass was greatest in the hedge and centre of the crop (Fig. 2a). Number of prey was highest in the hedge and the centre of the crop; however, these habitats did not harbour the same range of prey, with earthworms more numerous in the hedge than in the centre of the crop ($\chi^2 = 8.14$, d.f. = 2, $P < 0.001$) (Fig. 2b).

In summary, the number of available prey items decreased from the hedge to the centre of the crop (Fig. 1) but this did not reflect the situation for prey biomass or density, as there was high prey biomass at the centre of the crop.

Effectiveness of satiation-state manipulation

The mean initial weight was significantly higher for satiated than for starved beetles, however for satiated individuals there was an unexplained significant effect of enclosure (Table 1); the initial weight at the moment of release was lower for individuals released in enclosures situated in the mixed crop. This meant either that satiated individuals were not all in the same satiation-state condition at the beginning of the experiment (bias in the satiation-state manipulation) or that satiated individuals

released in the mixed-crop enclosures were by chance smaller in size than those released in the other enclosures.

In order to choose between the two possibilities, the relative initial weight was used, described by the ratio between initial weight and basal weight, $W_{0,SA,i}/W_{B,SA,i}$; this variable controls for the possible effect of size. The enclosure effect disappeared in analysis of relative initial weight (Table 1), indicating that differences in basal weight among enclosures were due to chance differences in individual body size rather than to differences in treatment efficiency. Thus, WR_i (ratio between mean basal weight and individual weight at recapture) was used in subsequent analyses to control for initial differences in body size and reveal real habitat effects.

Activity over the whole period

Analyses of non-cumulative frequencies of recapture on each day (Fig. 3) indicated that over all habitats on day 1, starved individuals were significantly more active than satiated individuals ($\chi^2 = 7.93$, d.f. = 1, $P < 0.001$). This satiation-state effect was not significant on subsequent days. On day 1, whatever the satiation-state group, beetles were also more active in the mixed crop and wheat crop margin habitats ($\chi^2 = 9.20$, d.f. = 3, $P < 0.05$). This habitat effect was not significant on subsequent days.

Activity and weight variation after 1 day

For starved individuals (Fig. 4), the amount of weight increase after 1 day did not differ significantly among habitats ($F = 0.13$, d.f. = 3, $P = \text{NS}$), however there was a significant habitat effect for frequencies of recapture ($\chi^2 = 10.22$, d.f. = 3,

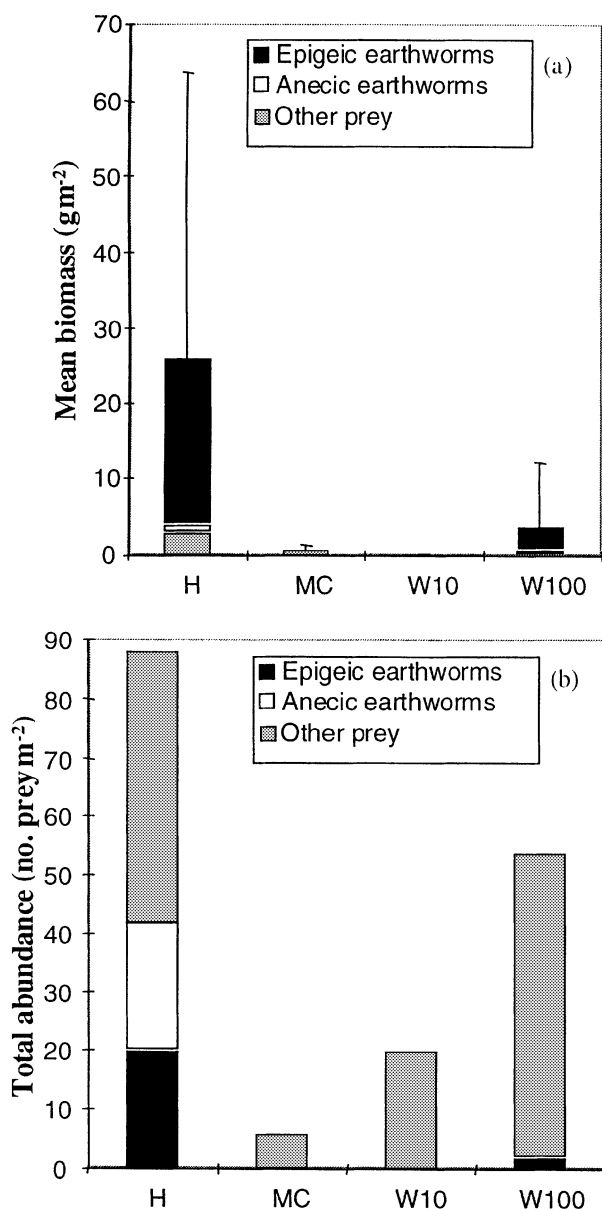


Fig. 2. Prey sampling by formaldehyde extraction in quadrats in the various habitats in July 1997. (a) Mean biomass per quadrat (g m^{-2}). (b) Total number of prey summed over all quadrats (no. of individuals m^{-2}). Collembola are not included. H: hedge, MC: mixed crop, W10: wheat crop margin, W100: wheat crop centre.

$P < 0.05$). From the hedge to the wheat crop margin, beetles were more and more active, but activity was very low in the centre of the crop. Hence, during the first 24 h, the four habitats were not used identically by starved individuals. For satiated individuals (Fig. 4), there was no significant habitat effect on either the amount of weight loss ($F = 0.79$, d.f. = 3, $P = \text{NS}$) or activity ($\chi^2 = 2.36$, d.f. = 3, $P = \text{NS}$). Hence, foraging activity in different habitats depended on satiation level.

Weight variation over the whole period

There was a significant difference between satiation-state groups in weight variation between recapture and release over all dates (Fig. 5). Whatever the day of recapture, starved individuals had gained weight ($\overline{\text{WR}}_{\text{ST}} = 1.149$, $\text{SD} = 0.207$) whereas satiated individuals had lost weight ($\overline{\text{WR}}_{\text{SA}} = 0.916$, $\text{SD} = 0.163$) ($F = 69.53$, d.f. = 1, $P < 0.001$). In both groups, there was a nearly significant effect of recapture date, showing that weight at recapture tended to increase with time ($F = 2.22$, d.f. = 5, $P = 0.0543$). Indeed, the later starved individuals were recaptured, the more weight they had gained, whereas the later satiated individuals were recaptured, the less weight they had lost in comparison with the original state (Fig. 5). There was no significant effect of habitat on changes in weight.

Discussion

The four habitats differed according to prey availability. Prey was abundant and diverse in the hedge, and abundant but not diverse in the crop centre. This gradient of prey availability reflects the local characteristics of the studied habitats, hence it cannot be generalised. It seems consistent with several other studies (Lewis, 1969; Nentwig, 1988), however, indicating that this decrease in prey availability with the distance to undisturbed habitats may be encountered frequently at field margins.

The first aim of this work was to test the hypothesis about the influence of hunger on carabid foraging activity (Grüm, 1971a; White, 1978; Baars, 1979; den Boer, 1986). This hypothesis can be viewed as a behavioural continuum (directed walk \rightarrow random walk \rightarrow inactivity) associated with a continuum of hunger levels (totally starved \rightarrow partially satiated \rightarrow totally satiated). There is little experimental evidence for this relationship, however, especially in natural conditions, for insects in general (Evans, 1976) and for carabid beetles in particular (Grüm, 1971b; Lenski, 1984; Mols, 1987, 1988). According to this hypothesis, starved individuals were expected to have a high initial level of activity (due to their expected displacement behaviour, directed walk, which should enhance their probability of falling into a trap). This level of activity should decrease progressively with time (as beetles' satiation increases and their displacement behaviour switches towards random walk), and finally reach a plateau, when an optimal foraging strategy is reached (foraging at equilibrium). On the contrary, satiated individuals should have a low initial level of activity, which increases with time (as their digestion progresses and their hunger increases) up to a plateau. The final activity level should be the same in satiated and starved groups (which should correspond to foraging at equilibrium). The overall results for activity (Fig. 3) indicate that starved beetles were more active than satiated beetles at the beginning of the experiment, and that this difference disappeared with time. For starved beetles, 48 h of high activity seemed to be enough to reach better nutritional status satiation conditions in the habitats studied. For satiated individuals, the probability of

Table 1. Efficiency of manipulation of initial hungry state for *Pterostichus melanarius*. $W_{0,i}$: initial weight of individual i at the moment of release, $W_{0,ST,i}$: initial weight of starved individual i after 6 days of starvation ($W_{0,ST,i} = W_{B,ST,i}$), $W_{0,SA,i}$: initial weight of satiated individual i after last meal, $W_{B,SA,i}$: basal weight of satiated individual i after 6 days of starvation.

Hungry-state group	Dependent variable	Independent variable	n	F	P	d.f.	r^2	Mean \pm SD
Both	$\log(W_{0,i})$	Group	258	141.42	0.0001	1	0.356	$W_{0,SA} = 0.223 \pm 0.031$ g $W_{0,ST} = 0.173 \pm 0.038$ g
Starved (ST)	$\log(W_{0,ST,i})$	Enclosure	128	0.76	0.618	7	0.042	
Satiated (SA)	$W_{0,SA,i}$	Enclosure	130	2.46	0.021	7	0.125	
Satiated (SA)	$W_{0,SA,i}/W_{B,SA,i}$	Enclosure	130	0.95	0.05	7	0.052	

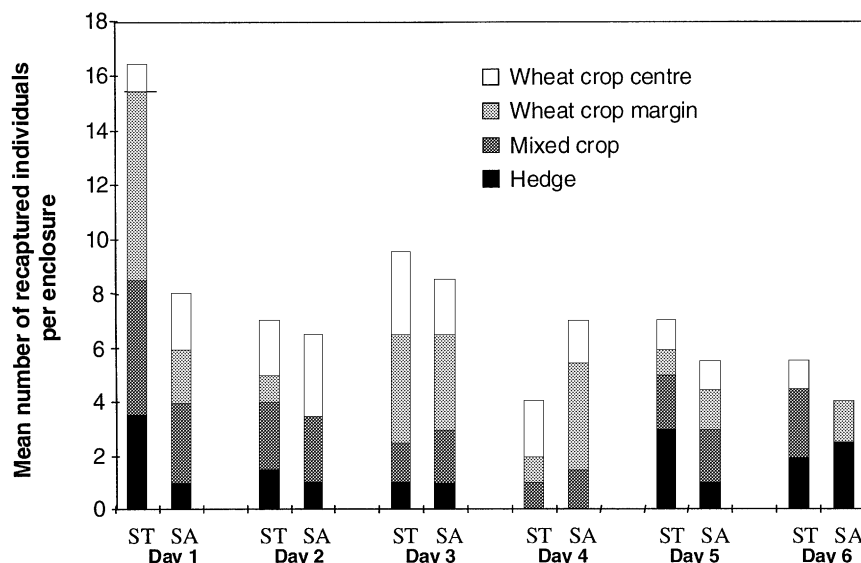


Fig. 3. Numbers of recaptured *Pterostichus melanarius* on each day in the various habitats. SA: satiated group, ST: starved group.

recapture was low throughout the experiment; Pollet and Desender (1990) argued that *P. melanarius* teneral could remain inactive for 3 or 4 days during the digestion of a complete meal. In this experiment beetles were not sexed, however the experiment was conducted outside the reproductive period, so that differences in foraging activities between males and females should be reduced.

As regards weight changes in starved individuals (Fig. 5), the weight ratio between release and recapture was always > 1 (after 24 h: $WR_{ST} = 1.12 \pm 0.20$ SD; Student test: $t = 3.47$, d.f. = 32, $P = 0.001$). Also, whatever the satiation-state group, the longer a beetle remained in the enclosure, the more weight it gained, probably reflecting a higher chance of finding food. This result may be explained for starved individuals according to the above hypothesis: this group of individuals may be very active at the beginning of the experiment, their motivation being the search for food. Among them, those that were not able to find any food (or only very little prey) should have a higher probability of being trapped at the beginning of the experiment; in parallel, their weight should not increase, or

increase only very slightly, between release and recapture. On the contrary, starved individuals that were able to find a sufficient amount of food at the beginning should rapidly reach a lower level of activity. Thus, this category of beetles should be recaptured later with a higher weight, hence with a higher value of the weight ratio between release and recapture. This may explain the observed weight ratio curve, slightly > 1 at the beginning, then increasing as the experiment progresses. For satiated beetles the value of the weight ratio was < 1 after 24 h ($WR_{SA} = 0.84 \pm 0.13$ SD; Student test: $t = 4.94$, d.f. = 15, $P = 0.001$). This may correspond to those initially satiated individuals that have digested rapidly. Afterwards it increased towards 1, and did not differ significantly from this value from day 4. A possible explanation of this pattern may be that prey availability is sufficient that the foraging activity of satiated individuals reaches equilibrium from day 4.

Overall, the results for both activity and weight variation support the idea that, at least at the beginning, starved individuals are more active than satiated individuals because of foraging.

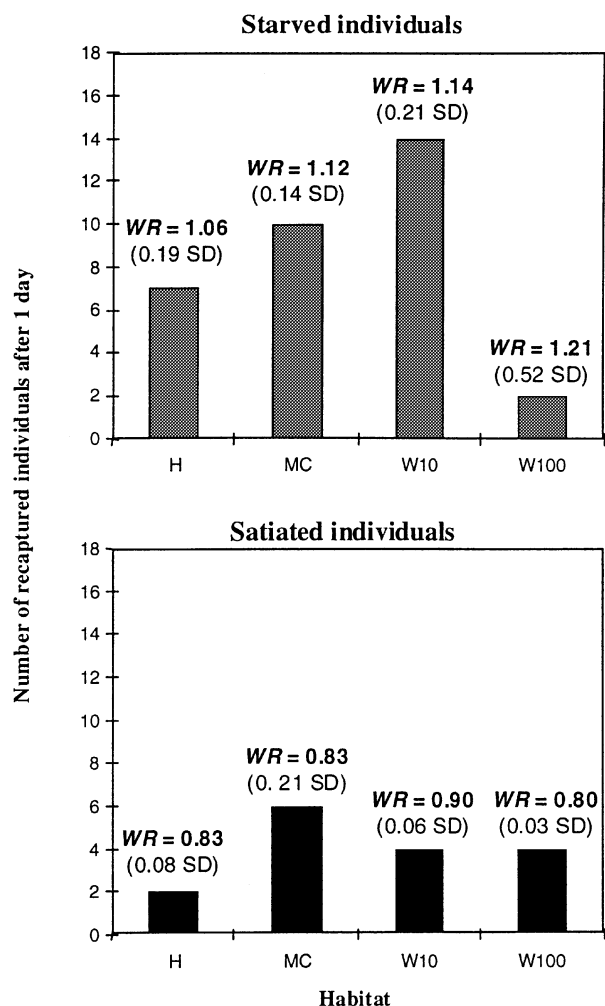


Fig. 4. Numbers of recaptured individuals at day 1 for each satiation-state group in the various habitats, and related values of weight ratio between release and recapture (*WR*). The effect of habitat on activity was significant for starved individuals only ($\chi^2=10.22$, d.f.=3, $P<0.05$). The effect of habitat on weight ratio was not significant in any group. H: hedge, MC: mixed crop, W10: wheat crop margin, W100: wheat crop centre.

A significant effect of habitat on activity after 24 h was also observed for starved individuals only (Fig. 4). In the centre of the wheat crop, few starved individuals were active after 24 h. Possibly starved beetles are not active at foraging in this habitat because conditions are somehow adverse. Several authors have argued that vegetation and soil structure or temperature influence activity, as monitored by pitfall traps, more than satiation level (Cárcamo & Spence, 1994, and references therein). *Pterostichus melanarius*, which is a night-active carabid, however, may be less affected by variation in temperature, as the range of variation is more extreme during the day. Moreover, patterns of activity differed significantly between the margin and the centre of the wheat crop (Fig. 4),

although these two areas are likely to offer almost identical microclimatic conditions. More important, if in the centre of the crop hunger levels were of negligible importance in determining activity in comparison with abiotic adverse conditions in the centre of the crop, starved individuals should not have gained weight after 24 h.

Hence, the hunger-dependent foraging hypothesis seems to apply in the centre of the crop. Perhaps the foraging strategy of starved individuals is more efficient in the crop centre than elsewhere. In other words, the early foraging activity of starved beetles just after release, hypothesised to be a directed walk strategy, would allow efficient prey capture, and thus starved beetles would rapidly (<24 h) adopt a random walk strategy, leading to lower rates of recapture in pitfall traps. This explanation remains speculative because individual displacements were not studied in this experiment, however several arguments support the idea that directed walk should lead to higher foraging efficiency in the centre of the crop than in the hedge. First, the centre of the crop is characterised by a very simple and regular vegetation structure and ground cover. Several authors have suggested that directed walk is favoured by these habitat features because there are few obstacles on the soil surface (Ericson, 1978; Hance, 1990; Kennedy, 1994). Also, microclimatic conditions are regular but harsh, with high day–night temperature differences and high potential for desiccation. Speight and Lawton (1976) showed that within a crop, *P. melanarius* avoids bare areas because of this microclimatic constraint. Wallin and Ekbohm (1988) suggested that this could force the beetles to adopt a directed walk behaviour. As a direct consequence of the observed gradient in prey availability among habitats (see also Lewis, 1969; Nentwig, 1988), prey diversity is reduced in the centre of the crop but prey abundance and biomass remain rather high. Because of the regularity of soil and vegetation conditions, prey are also likely to be distributed more regularly in this habitat. Note, for example, that the standard deviation of prey biomass (Fig. 2a) was lower in the centre of wheat crop than in the hedge. Hence, in the crop centre foraging beetles may encounter few prey items that are abundant and distributed regularly. From a theoretical point of view, Dunsberry (1989) argued that directed walk gives the best results when prey are distributed regularly. All these arguments favour the idea that in the crop centre, directed walk may be either the preferred or the obligatory initial displacement behaviour for starved *P. melanarius*.

In summary, directed walk should be not only the favoured strategy for starved *P. melanarius* in the crop centre because of abiotic conditions and the beetle's specific habitat preferences, but this strategy should also give the highest food intake efficiency because of the particular patterns of prey availability. In contrast, high activity linked to directed walk may be hampered in the hedge by the complexity of vegetation structure (Grüm, 1971b). Indeed, a trend was observed towards lower activity and lower increase in weight for starved individuals in the hedge after 24 h (Fig. 4). Thus the hedge is probably not the best habitat for starved *P. melanarius*. When the beetles are satiated, however, the hedge is likely to be very favourable as it offers a lot of refuges where beetles could

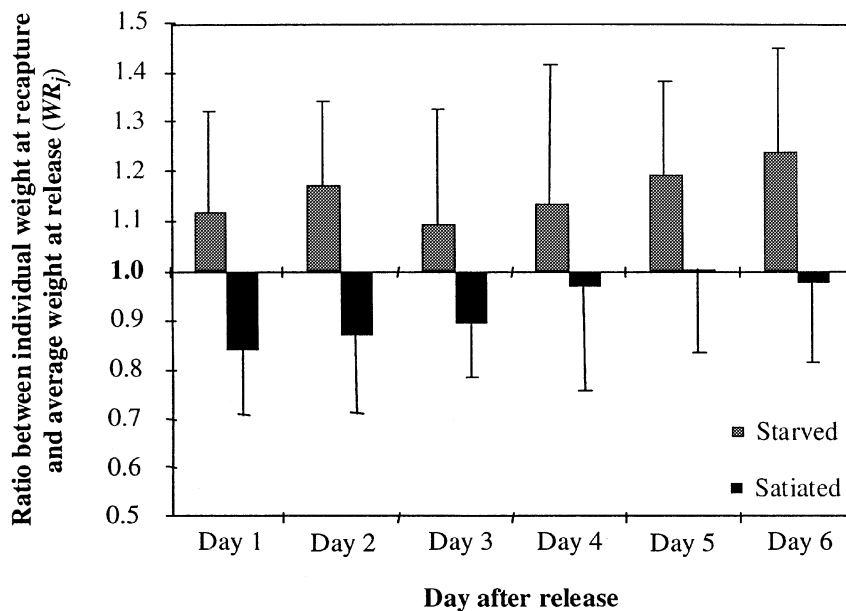


Fig. 5. Weight ratio between recapture and release (WR) and SD, for each satiation-state group and each date. The effect of satiation-state group was significant ($F=69.53$, d.f. = 1, $P<0.001$); the effect of date was almost significant ($F=2.22$, d.f. = 5, $P=0.0543$).

remain inactive for a long time. Activity of satiated individuals after 24 h actually tended to be lower in the hedge. Nevertheless, because the experimental design is limited to two adjacent hedgerows, these results may only be due to local characteristics of the studied habitats. Hence, extensions to hedge/field systems in general have to be considered cautiously.

This overall discussion points out the fact that foraging strategies, which mainly determine spring activity of *P. melanarius*, can rather be viewed as the result of interaction among three main internal and external factors: the satiation level of the beetle, prey availability in the habitat, and the physical structure of the habitat that is related directly to the beetle's habitat preferences. Depending on these interactions, *P. melanarius* may exploit the available habitats differently; in particular, in the local conditions of the study, the centre of the crop seems to be the most favourable habitat for *P. melanarius* individuals to find food rapidly. This species may thus prefer the centre of the cereal crop for foraging. Hedge species interacting with adjacent fields have been described in the literature (Pollard *et al.*, 1974). Indeed, species in hedgerows have a closer resemblance to woodland species assemblages and generally interact little with adjacent cultivated areas (Charrier *et al.*, 1997; Petit & Burel, 1998). Conversely, *P. melanarius* may be a field species interacting with hedges in particular conditions, especially when hedges are young and low. This hypothesis requires further investigation with respect to displacement from one habitat to another, and a generalisation to other hedge/field systems.

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