

Movement of *Pterostichus melanarius* in agricultural field margins in relation to hunger state

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Abstract

We studied the foraging activity of *Pterostichus melanarius* in three habitats near a field margin : a hedge, a transition crop, and a cereal culture edge. In a first experiment, starved and satiated beetles were released in enclosures within each habitat. In a second experiment, starved and satiated individuals were released in larger enclosures, where they were free to move between the above habitat types. Results of both experiments showed that starved individuals were more active than satiated ones, probably because of foraging. Experiment 1 showed that the crop centre was the habitat where starved beetles were the most efficient in foraging. Experiment 2 showed that when free to move from one habitat to another, starved individuals moved mostly towards the crop edge. *P. melanarius* exhibits a flexible habitat use, depending on three hierarchical factors : hunger, prey availability, and specific habitat preferences.

Keywords: *Pterostichus melanarius*, foraging strategy, agroecosystem, hedges.

1. Introduction

In intensively cultivated agroecosystems, the importance of undisturbed field margins for the maintenance and increase in populations of predatory arthropods is widely recognised (Maelfait *et al.* 1988; Nentwig 1988; Desender *et al.* 1989; Duelli 1990; Chiverton and Sotherton 1991; Hassal *et al.* 1992; Thomas *et al.* 1992a; Zangger 1994). Ground beetles have often been used to understand the ecological impact of habitat heterogeneity created

by such field boundaries (Burel 1989, 1992; Lys 1992, 1994; Thomas *et al.* 1992b; Rykken *et al.* 1997). In a previous study (Fournier and Loreau 1999), we showed that the diversity of carabids declined significantly with increasing distance from a recently established hedge towards field centre. The various species had different distribution patterns, indicating different habitat choice strategies. *Pterostichus melanarius* Ill., the most abundant species, exhibited a relative indifference towards the presence of the hedge, and a slight preference for the adjacent crop

field. This species is known to prey on crop pests such as aphids or slugs (Sunderland 1975; Sunderland and Vickerman 1980; Pollet and Desender 1985, 1986, 1987, 1990; Carcamo and Spence 1994; Symondson 1997). Understanding its foraging behaviour, and how it may be modulated by newly established habitats at field margins, is an important question. However, there are few experimental studies addressing this under field conditions.

Activity and habitat choice in insects are under the control of both abiotic and biotic factors (Thiele 1977; White 1978; Evans 1990; Lövei and Sunderland 1996). Several authors hypothesised that carabid foraging activity was mostly motivated by hunger (Grüm 1971a, 1971b; Baars 1979; Mols 1982, 1987; den Boer 1986). This hypothesis states that displacements are modified by prey intake. Just after prey is eaten, tortuous walk is adopted. This is followed by random walk, then directed walk if no prey is found. A totally satiated insect remains inactive during the beginning of the digestion process. This hypothesis thus recognises two main hunger states (starved and satiated), and assumes that (1) starved individuals are more active than satiated ones, and (2) this activity is due to foraging. However, habitat features also play a role. Prey density and diversity directly influence the hunger state, hence activity. In addition, both microclimatic conditions and the physical structure of the vegetation influence the beetle's ability to move within a particular habitat, its sensitivity to prey stimuli, and its movement from one habitat to another (Cárcamo and Spence 1994, and references cited therein).

Our study site offers the possibility to understand the foraging strategies of *P. melanarius* in a mosaic of newly established field margin habitats: a hedge, a transition zone and the crop field itself. These habitats offer a gradient of physical structure, disturbance level and prey availability. We aimed to answer three main questions: (1) Does hunger-state influence *P. melanarius* activity within the habitats studied? (2) Is this relationship different among habitats, and if yes, what are the main factors modifying it? (3) What are the consequences of this behaviour on the between-habitat movement of *P. melanarius*?

We performed two capture-recapture experiments, both based on the manipulation of initial hunger level of adult *P. melanarius*. Starved and satiated beetles were released in circular enclosures installed within each habitat in experiment 1, and in larger enclosures where they were free to move from one habitat to another in experiment 2.

2. Materials and methods

The experimental farm was situated in the intensively cultivated French region of Beauce (48°22' N, 1°45' W). Hedges were planted during the winter 1994-1995, as described in detail in Fournier and Loreau (1999). They were composed of two elements: (1) shrubs 200 m long and 6 m wide and (2) a 100 m long mixed crop (oats, cabbages and buckwheat). Two blocks of shrubs were separated by the block of mixed crop. 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 on all sides. We distinguished four habitat categories running at right angle from this sequence: the hedge, the mixed-crop edge, and two categories in the winter wheat crop: the "margin" (a 10 m wide strip at the edges) and the "centre" (areas 100 m away from the margin). The habitats differ according to the physical structure of vegetation (complexity sequence: hedge > mixed crop > wheat crop) and according to the level of disturbance (hedge: undisturbed; mixed crop: little disturbed; wheat crop margin and centre: frequently disturbed by prevailing agricultural practices). As a consequence, the hedge is likely to offer more refuge opportunities and a greater prey diversity than the other habitats (Lewis 1969; Fournier and Loreau 1999).

We employed two different methods for measuring prey availability. We captured ground-dwelling animals with pitfall traps installed at increasing distances from the hedge (4 traps at each distance from April to July 1996). We identified insects to the family level, except for Collembola. Other groups of invertebrates (Araneids, Annelids,

Molluscs, Myriapods) were also captured but were not counted. We also performed formaldehyde extractions in quadrats (8 in each habitat in July 1997), by moistening a quadrat of soil (25 cm x 25 cm) with a 0.04% solution of formaldehyde twice during 20 minutes (Guillemain et al. 1997). We distinguished four groups of animals (epigeous, anecic and endogeous earthworms, and other prey). Each prey was allocated to one of these groups, and weighed to the nearest mg (except Collembola). We used the first method to illustrate differences in prey diversity among habitats, and the second one to describe variations in prey densities and fresh biomass.

The carabid species studied, *P. melanarius*, is a nocturnal autumn breeder, 12-18 mm long (Jeannel 1941, 1942; Greenslade 1965; Thiele 1977; Lindroth 1974, 1992). It is eurytopic but mainly prefers open habitats, and is favoured by agriculture (Desender and Alderweireldt 1988). Besides the autumnal reproductive period (August-September), June is another period of high activity corresponding to the emergence of teneral adults that actively forage (Fadl et al. 1996). *P. melanarius* has a very non-specific diet (Pollet and Desender 1985), including numerous crop pests (Sunderland 1975; Sunderland and Vickerman 1980; Pollet and Desender 1987). It seems to be an opportunistic predator, feeding on the most common available prey type, be these insects (Pollet and Desender 1986, 1987) or slugs (Symondson 1997, pers. comm.). *P. melanarius* tolerates different rearing conditions (Tomlin 1975; Ericson 1977). We did not check for homogeneity of samples with respect to age class and sex, which could influence food intake and activity (Makowski and Szyszko 1986). The experiment, conducted in June 1997, was not performed during the reproductive period, so that differences between sexes in activity and food intake were probably negligible.

In both experiments, the beetles were hand-collected in the field and held in individual plastic boxes with a thin layer of soil and a filter paper which was moistened daily. They were maintained at ambient temperature, and fed every 4 days with earthworms. During all the manipulation water was given *ad libitum*. Before the pre-release treatment, all beetles were starved for 6 days. After starvation

they were weighed (to the nearest mg: basal body mass of individual $i = W_{0,i}$). Beetles were separated into 2 hunger groups: starved and satiated. Satiated individuals were fed with earthworms *ad libitum* for 24 hours, while starved individuals were not fed. The beetles were marked on the elytra using a micro-drill (Loreau 1984). One day later, satiated insects were re-weighed. We called $W_{0,g,i}$ the initial body mass of individual i of hunger group g . Starved individuals were not weighed again before release.

Experiment 1

In each of the 4 habitats, we installed two circular enclosures (diameter 5 m) 500 m apart (Fig. 1). They were made of plastic sheets 50 cm high, vertically maintained with stakes, and buried in the soil 10 cm deep. Eight pitfall traps were evenly spaced along the interior wall. The experiment was performed with 128 starved and 130 satiated *P. melanarius*, with equal numbers of starved and satiated individuals released on day 0 in each enclosure. After release, traps were checked every day for 6 days. The mark of each recaptured individual j was determined under a binocular lens, the beetle was weighed, then 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, and analysed as a function of hunger group, habitat and date. We called $W_{C,j,g,k}$ the body mass at recapture of individual j , belonging to hunger group g , and recaptured in enclosure k . It was not possible, in this first experiment, to follow the variation in body mass of individual beetles, because they did not carry individual marks. We thus calculated the mean initial body mass of each hunger group g in each enclosure k , and used it as the initial body mass for group g in enclosure k . The ratio between the recapture body mass of individual j and the mean initial body mass of the group in each enclosure, was calculated as:

$$\overline{WR}_j = \frac{W_{C,j,g,k}}{W_{0,g,k}} \quad (\text{eq. 1.})$$

This variable was used to study the changes in body mass between release and recapture (the length of this period may be 1 to 6 days).

Experiment 2

We installed two rectangular enclosures (21 m 6.5 m), made of plastic sheets 50 cm high, vertically maintained with stakes and buried in the soil 10 cm deep. Because of interference by agricultural machines, it was not possible to include the centre of the wheat crop (Fig. 1). Sixteen pitfall traps were evenly spaced along the interior border of each enclosure (mean distance between two traps : 3.4 m, *s.d.*=0.3 m), with one trap at each corner. The experiment was performed with a total of 127 starved and 128 satiated *P. melanarius*. On day 0, we released equivalent numbers of beetles of each hunger group in the centre of each habitat-type areas. We visited the enclosures for 8 days. Recaptured individuals were weighed, then released in the enclosure 20 cm from their trap of recapture.

We first analysed the number of recaptures per individual using a non-parametric Kruskal-Wallis test (because of non-normality of data). We also analysed the mean time of first recapture by fitting a logistic regression to the data of first recaptures as a function of date. Notation:

- N the initial number of released individuals,
- d the number of days after release ($d = 0$ being the day of release),
- P_d the probability of being recaptured for the first time on day d ,
- k the recapture rate,
- R_d the number of newly recaptured individuals at day d .

If we suppose that the recapture rate k is constant in time, and that there is no mortality over this short period of 8 days, the mean time of first recapture, T becomes :

$$T = \sum_{d=1}^{\infty} dP_d = \sum_{d=1}^{\infty} dk(1-k)^{d-1} = \frac{1}{k} \quad (\text{eq.2})$$

The number of newly recaptured individuals on day d is given by the following equation :

$$R_d = Nk(1-k)^{d-1} \quad (\text{eq.3})$$

k was estimated by fitting this logistic regression equation to the number of newly recaptured individuals as a function of the number of days between release and first recapture. Some days no individuals were recaptured ; we

considered these $R_d = 0$ as missing values. The analysis was done for each hunger group, in each enclosure and on the pooled data of the two enclosures. We performed Student's t - tests to compare k values using the estimate and asymptotic standard error of k .

In the second experiment insects were marked individually. We called $W_{d,i}$ the body mass of individual i at day d . WR_i was then defined as the ratio between the body mass at first recapture and the initial body mass:

$$WR_i = \frac{W_{d,i}}{W_{0,i}} \quad (\text{eq.4.})$$

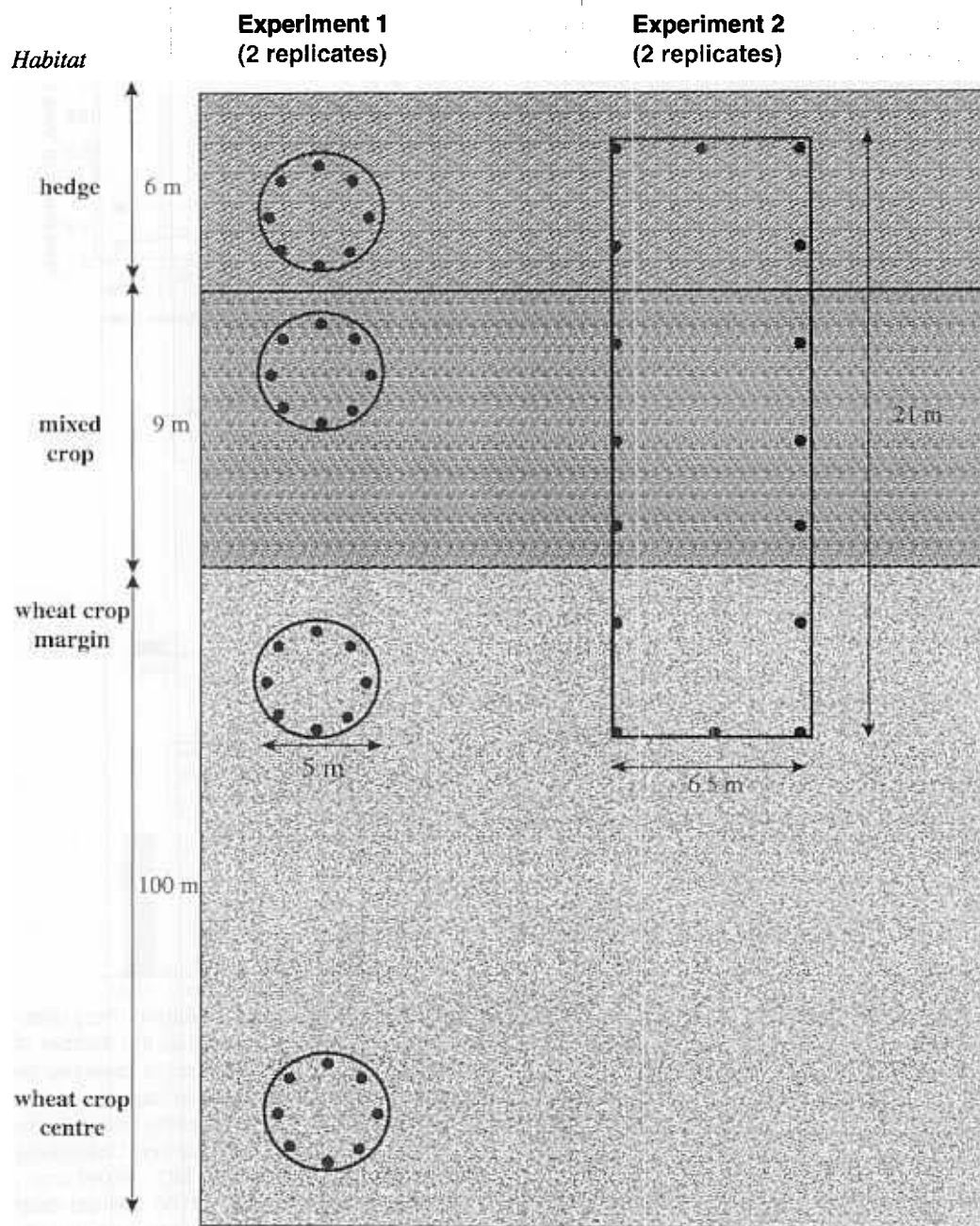
The relationships between body mass variation and hunger group was analysed using contingency table, with two classes considered for WR ($WR > 1$: gain of body mass, $WR < 1$ loss of body mass), and frequencies summed over both enclosures. We also used nested ANOVA models to analyse the relationship between WR and hunger group and initial habitat type, but for normalisation of data we had to work with the variable $1/WR$.

We analysed the locality of first recapture (hedge, mixed crop or wheat crop), as a function of hunger group and initial habitat type using contingency tables. We also distinguished different type of displacements between release and first recapture (« transition types »: « 0 » when individuals were recaptured in their initial habitat type, « 1 » when they were recaptured in another habitat type), and analysed this variable in the same way. Considering all recapture events together, we used contingency tables in order to analyse the frequencies of displacements towards each habitat type (hedge, mixed crop, wheat crop margin), as a function of the number of recaptures per individual and the hunger group.

3. Results

3.1. Prey availability in each habitat

Analyses of catches in pitfall traps between April and July 1996 showed that the number of individuals in each category (Tetanoceridae, Staphyli-



● pitfall traps

Figure 1. Experimental design of enclosures in experiment 1 and 2.

nidae, Formicidae, Jassidae, Bibionidae, Sciaridae, Scathophagidae, other Coleoptera, other Diptera, other Hymenoptera, other Hemiptera + Diptura),

differed significantly between habitats ($\chi^2 = 679$, $df. = 30$, $p < 10^{-5}$). Prey diversity was maximum in the hedge, minimum in the mixed crop, and remained

low in the cereal crop (Fig. 2.a). Formaldehyde extractions indicated significant variation among habitats in the total number of prey caught ($\chi^2 = 96.2$, $d.f. = 3$, $p < 10^{-5}$): number of prey were highest in the hedge and the crop centre (Fig. 2.b). These habitats, however, did not present the same range of prey: earthworms were more numerous in the hedge than in the centre of the crop ($\chi^2 = 8.14$, $d.f. = 2$, $p = 0.0043$). This was consistent with result on total prey biomass (Fig. 2.c).

3.2. Experiment 1

3.2.1. Activity and body mass variation over the whole period

On day 1, in all habitats, starved individuals were significantly more active than satiated ones ($\chi^2 = 7.93$, $d.f. = 1$, $p = 0.0048$). This effect was no longer significant on subsequent days. On day 1, whatever the hunger group, beetles were also more active in the mixed crop and the wheat crop margin ($\chi^2 = 9.20$, $d.f. = 3$, $p = 0.0268$), but again this habitat effect was no longer significant on subsequent days.

Whatever the day of recapture, recaptured starved individuals had gained body mass ($\bar{W}R_{ST} = 1.149$, $s.d. = 0.207$), whereas satiated individuals had lost body mass ($\bar{W}R_{SA} = 1.149$, $s.d. = 0.163$) ($F = 69.53$, $d.f. = 1$, $p = 0.0001$). There was no significant effect of habitat.

3.2.3. Activity and body mass variation after 24 h

For starved individuals (Fig. 3), the amount of mass increase after one day did not differ significantly between habitats ($F = 0.13$, $d.f. = 3$, $p = 0.94$). However, from the hedge to the wheat crop margin, beetles were more and more active. Activity was very low in the centre of the crop ($\chi^2 = 10.22$, $d.f. = 3$, $p = 0.0168$). Hence, during the first 24 h, the four habitats were not used identically by starved individuals. For satiated individuals (Fig. 3), there was no significant habitat effect on either the amount of body mass loss ($F = 0.79$, $d.f. = 3$, $p = 0.53$), or activity ($\chi^2 = 2.36$, $d.f. = 3$, $p = 0.50$). Hence, the relationship between activity due to foraging and hunger level of the insect differed in the different habitat type.

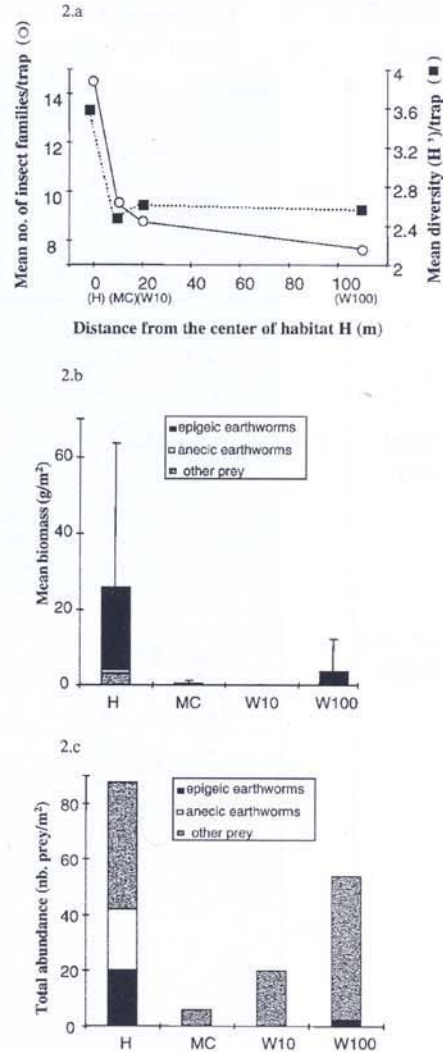


Figure 2. Variations in prey availability. Prey diversity (Figure 2.a) was measured as the number of insect families (○) and Shannon's diversity index (■) in pitfall traps (means per trap), as a function of distance from the centre of the hedge (sampling in spring 1996). Carabidae and Collembola were not included. H: hedge; MC: mixed crop; W10: wheat crop margin; W100: wheat crop centre. Prey biomass (Figure 2.b) and density (Figure 2.c), were measured using sampling by formaldehyde extraction in July 1997. Figure 2.b: mean biomass per quadrat in g/m². Figure 2.c: total number of prey summed over all quadrats, numbers of individuals/m². Collembola were not included. H: hedge; MC: mixed crop; W10: wheat crop margin; W100: wheat crop centre.

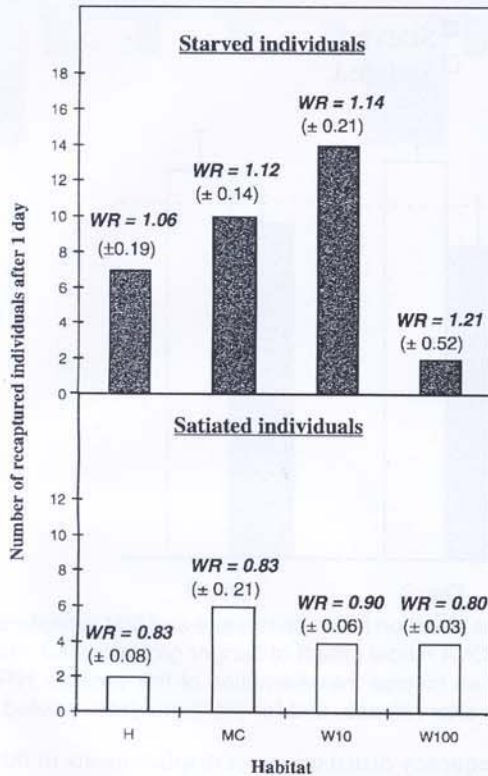


Figure 3. Numbers of recaptured individuals at day 1 for each hunger group in the various habitats in experiment 1, and related values of body mass ratio between release and recapture (WR) (standard deviation between brackets). Grey: starved group, black: satiated group. The effect of habitat on activity was significant for starved individuals only ($\chi^2 = 10.22$, $d.f. = 3$, $p = 0.0168$). The effect of habitat on body mass ratio was not significant in any group. H: hedge; MC: mixed crop; W10: wheat crop margin; W100: wheat crop centre.

3.3. Experiment 2

3.3.1. Activity levels

The total number of recapture occasions per individual did not depend significantly on initial hunger state in any of the enclosures (Kruskal-Wallis non parametric test: $H = 0.54$, $d.f. = 1$, $p = 0.46$). The analysis of the mean time of first recapture showed that starved *P. melanarius* always tended to be recaptured earlier than satiated ones (Table 1). Student tests on k values showed that this difference was not significant in each enclosure separately (Student's t -test in enclosure E_1 : $t = 0.24$, $d.f. = 11$, $p = 0.41$; in enclosure E_2 : $t = 1.56$, $d.f. = 7$, $p = 0.08$), but it became significant when the logistic regression was fitted to pooled data from the two enclosures ($t = 1.71$, $d.f. = 20$, $p = 0.05$).

3.3.2. Body mass variation

The body mass variation depended significantly on initial hunger state: 15 starved and 50 individuals lost mass, while 34 starved and 11 satiated beetles gained body mass ($\chi^2 = 29.60$, $d.f. = 1$, $p < 0.0001$). The ANOVA (made on the variable $1/WR$) confirmed this result (Fig. 4), at least for recaptures on days 1 ($F = 256.22$, $d.f. = 1$, $p = 0.04$), day 2 ($F = 312.38$, $d.f. = 1$, $p = 0.04$), and day 3 ($F = 53.36$, $d.f. = 1$, $p = 0.02$).

3.3.3. Directions of displacements

The habitat type where individuals were recaptured for the first time (all dates of recapture confounded), did not depend significantly on

Table 1. Recapture rates (k), estimated by logistic regressions of the number of newly recaptured individuals as a function of the number of days between release and first recapture. The mean time of first recapture is given by $T = 1/k$.

Enclosure	Initial hunger state	Number of observations	Estimate of k	Asymptotic standard error of k	Related value of T
E1	Starved	6	0.131	0.030	7.640
	Satiated	7	0.126	0.039	7.928
E2	Starved	3	0.160	0.048	6.261
	Satiated	6	0.121	0.028	8.279
E1 + E2	Starved	9	0.141	0.024	7.074
	Satiated	13	0.124	0.023	8.083

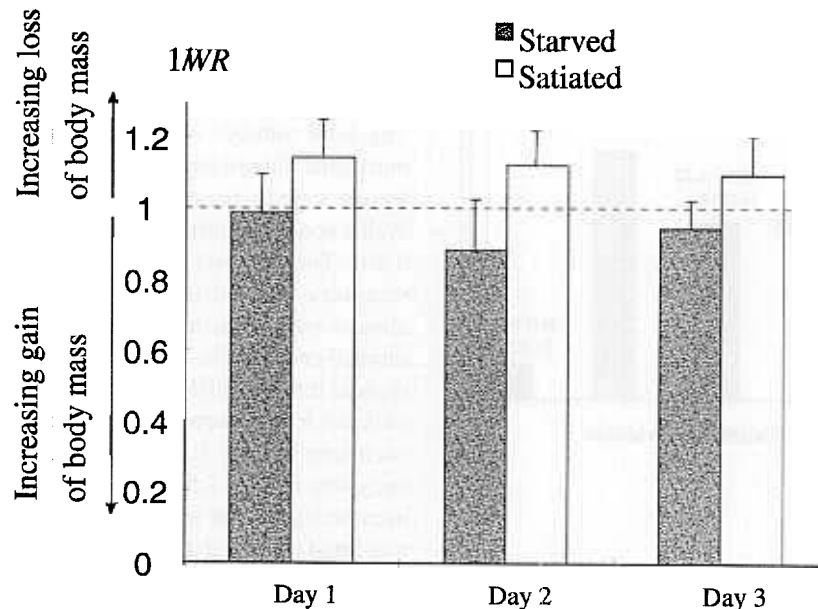


Figure 4. Effect of initial hunger state on the body mass variation between release and first recapture in experiment 2. The effect was tested in a nested ANOVA model (effect of hunger group nested into effect of enclosure), and data were normalised using an inverse transformation of the variable WR (). Analyses were performed separately for each day after release, and for the three dates pooled.

initial hunger state (enclosure E_1 : $\chi^2 = 0.77$, $d.f. = 2$, $p = 0.68$; enclosure E_2 : $\chi^2 = 0.92$, $d.f. = 2$, $p = 0.63$; pooled data: $\chi^2 = 1.83$, $d.f. = 2$, $p = 0.40$). However, there was a trend (although non significant) towards higher recaptures of starved individuals in the wheat crop margin, *versus* higher recaptures of satiated individuals in the hedge.

The transition type between release and first recapture (analysed with frequencies summed over the two enclosures, and all dates of first recapture included) depended significantly on the interaction between initial hunger state and initial habitat type (Fig. 5). Significantly more starved individuals left their initial habitat when they had been released in the hedge or the mixed crop ($\chi^2 = 5.86$, $p = 0.05$, $d.f. = 2$). Satiated individuals tended to leave their initial habitat more frequently when they had been released in the mixed crop (marginally significant trend: $\chi^2 = 4.55$, $d.f. = 2$, $p = 0.10$). However, the effect of initial hunger state alone was not significant ($\chi^2 = 0.69$, $d.f. = 1$, $p = 0.40$).

In total, 167 recapture events (first and subsequent ones) were observed (Table 2). The

frequency distributions of displacements in the various directions (towards the hedge, the mixed crop or the wheat crop margin) were significantly non-uniform ($\chi^2 = 16.78$, $d.f. = 2$, $p = 0.0002$): insects moved significantly more towards the hedge or the wheat crop margin. The effect of initial hunger state was not significant ($\chi^2 = 2.14$, $d.f. = 2$, $p = 0.34$).

4. Discussion

The four habitats differed according to prey availability: the number of available prey items decreases from the hedge to the centre of the crop (Fig. 2.a). This was not followed by a decrease in prey biomass and density (Fig. 2.b and 2.c), as the centre of the crop offered a high prey biomass. Prey was abundant and diverse in the hedge, and abundant but not diverse in the crop centre. This gradient of prey availability seems consistent with several other studies (Lewis 1969; Nentwig 1988) and appeared to be the most important factor distinguishing the four habitats.

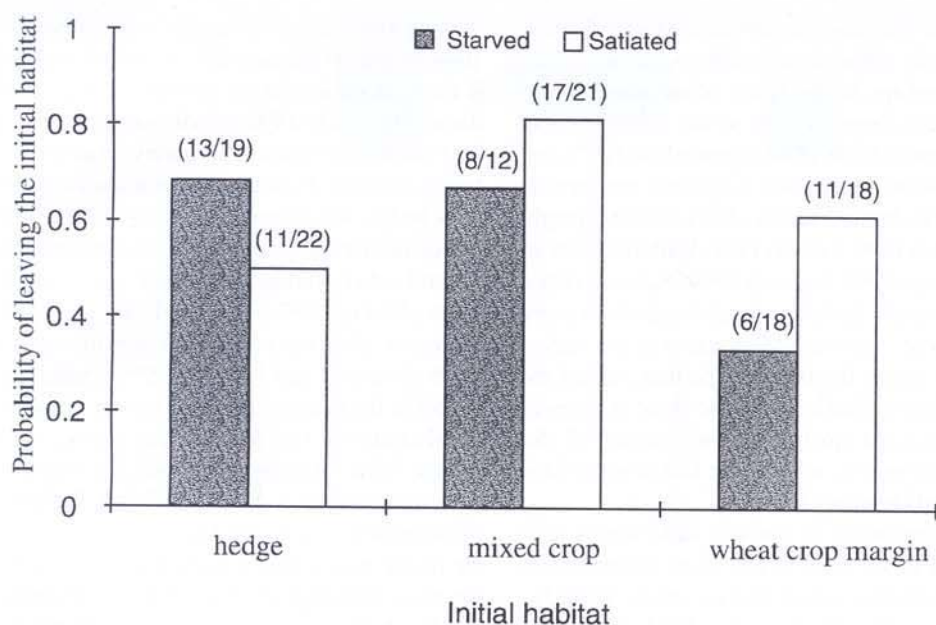


Figure 5. Probability of leaving the initial habitat between release and first recapture (irrespective of date), for the two hunger groups in experiment 2. Frequencies, summed over the two enclosures, are indicated in brackets.

Table 2. Frequencies of displacement in each direction (towards the hedge, the mixed crop or the wheat crop margin), for the two hunger groups during the whole experiment (all events of recapture considered). Frequencies were summed over the two enclosures.

Hunger group	Displacement towards ...			Total number of displacement events
	hedge	mixed crop	wheat crop margin	
Starved + Satiated	57	34	76	167
Starved	22	17	38	77
Satiated	35	17	38	90

The first aim of experiment 1 was to test the hypothesis about the influence of hunger state on carabid foraging activity, proposed by several authors (Grüm 1971a; White 1978; Baars 1979; den Boer 1986). This hypothesis can be viewed as a behavioural continuum (directed walk / random walk / inactivity) associated with a continuum of hunger levels (starved / partially satiated / totally satiated). However, there is little experimental evidence for this relationship, especially under natural conditions (Evans 1976; Grüm 1971b; Lenski 1984; Mols 1987, 1988). Results of experiment 1 indicated that starved beetles were more active than satiated ones at least at the beginning of the

experiment. This difference disappeared after 48 h. Starved individuals gained body mass during the whole duration of the experiment whereas satiated ones lost body mass. Both results supported the idea that, at least at the beginning, starved individuals were more active than satiated ones because of foraging. We also observed that, for starved beetles only, several individuals were still active after 24 h in the centre of the wheat crop (Fig. 3). Moreover, in this habitat the body mass gain tended to be the greatest (in average + 21 % of the mean initial body mass, non significant effect). It seems that starved individuals found a sufficient amount of food in 24 h. These results

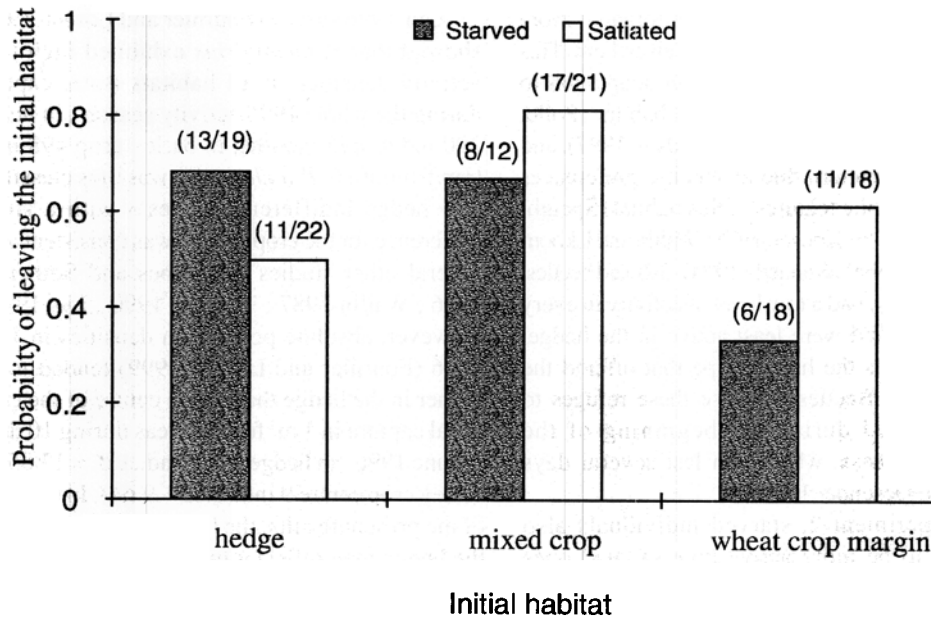


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suggested that starved individuals foraged more successfully in the crop centre than elsewhere. This would perhaps be the result of an adaptation to the reduced range of prey in this habitat (Pollet and Desender 1986, 1987; Symondson 1997), and a locomotion pattern due to specific preferences for several abiotic features of this habitat (Speight and Lawton 1976; Ericson 1978; Wallin and Ekblom 1988; Hance 1990; Kennedy 1994). Satiated beetles, on the contrary, had a low level of activity in every habitat type, and were least active in the hedge, although this is the habitat type that offered the most refuges. Beetles may use these refuges to stay protected during the beginning of the digestion process, which can last several days (Pollet and Desender 1990).

In experiment 2, starved individuals also appeared to be more active than satiated ones (lower mean time before first recapture, Table 1). In this experiment, starved individuals gained body mass whereas satiated ones lost body mass (Fig. 4). It also appeared that *P. melanarius*, whatever its initial hunger level was, followed two preferential directions: towards the hedge and towards the wheat crop margin. Starved individuals tended to be more frequently recaptured for the first time in the wheat crop margin. Also, the probability of leaving its initial habitat type between release and first recapture was higher for starved beetles released in the hedge or the mixed crop: these beetles probably moved towards the wheat crop margin (Fig. 5). Displacements of satiated individuals between release and first recapture seemed to be less directional.

Hence, *P. melanarius* seemed to exhibit a flexible habitat use for foraging, and this behaviour may be under the control of three main interacting factors: the beetle's hunger level, the prey availability in the habitat and the specific habitat preferences of this carabid species. Both experiments were conducted within a short period of time and with only two repetitions. Results thus have to be considered cautiously before generalisation. They still add significant information to the knowledge of foraging in carabids.

Our 1996 survey (Fournier and Loreau 1999) showed that *P. melanarius* exhibited high total activity densities in all habitats (total capture during the whole 1996 activity season: in hedge 290 ind./trap/5 months; in barley crop 498 ind./trap/5 months). *P. melanarius* was thus classified as « hedge indifferent species » with a slight preference for the crop, which was consistent with several other studies (Coombes and Sotherton 1986; Wallin 1987; Thomas 1990; Lys 1992). However, absolute population densities in June 1996 (Fournier and Loreau 1999) tended to be higher in the hedge than in the centre of the crop (total capture in 1 m² fenced areas during 10 days in June 1996: in hedge 17.42 ind., s.d. = 13.85; in barley crop centre 9 ind., s.d. = 9.64). In the light of the present results, the high activity density in the hedge may reflect a high population density but a low foraging activity (if the beetles present in the hedge are effectively satiated or reproducing individuals), whereas in the crop, the high activity density may reflect a high activity due to foraging, but a lower population density.

Foraging strategies, that mainly determine spring activity of *P. melanarius*, can be the result of the interaction between three main factors: the hunger level of the beetle, the prey availability in the habitat, and the physical structure of the habitat. *P. melanarius* individuals may exploit the available habitats differently. The centre of the crop seems to be the most favourable habitat for starved individuals that have to find food rapidly, and, when free to move between habitats, such starved individuals move towards the crop edge. If these results are confirmed by more extensive experiments, this can have interesting consequences for the management of field margins to enhance the biological control of pests. Indeed, our results on prey diversity in the different habitats showed that polyphagous and parasitic insects were evenly distributed, phytophagous insects were more abundant in the crop, and predatory insects were more abundant in the hedge (ratio phytophagous / predatory or parasitic: 0.714 in the hedge, 1.167 in the wheat crop margin, 1 in the wheat crop centre; $\chi^2 = 432$, d.f. = 9, $p < 10^{-5}$). This was also reported by

Nentwig (1988). If starved *P. melanarius* prefer this habitat for foraging, they exert predation pressure on these crop pests during crop infestation. On the contrary, other predatory species that show a marked preference for the hedge (like, in our case, *Pterostichus cupreus*, see Fournier and Loreau 1999), may be useful to control the numbers of pest species that use the hedge as a refuge.

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