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Short communication

Foraging activity of the carabid beetle *Pterostichus melanarius* Ill. in field margin habitats

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Abstract

The foraging activity of the carabid beetle *Pterostichus melanarius* was studied in a capture–recapture experiment in field margin habitats. Two rectangular enclosures were installed over a succession of habitats with a decreasing prey availability: a hedge, a mixed crop strip and an adjacent crop culture. Marked starved and satiated individuals were released in the enclosures and recaptured during 8 days. Initial satiation state had a significant effect on activity. Also, the initial displacements of beetles depended both on the habitat and on the initial satiation state. *P. melanarius* appeared to have flexible habitat-use, depending mainly on three factors: the satiation state, the habitat preference of the species, and the prey availability in the habitat. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Capture–recapture; Carabidae; Field margins; Foraging; *Pterostichus melanarius*; France

1. Introduction

Research in sustainable agriculture has stressed the importance of undisturbed field margins in intensive agro-ecosystems for the maintenance and enhancement of populations of predatory arthropods (Duelli, 1990; Hassal et al., 1992). Ground beetles (*Coleoptera*, Carabidae) have often been used to study the ecological effects of such field boundaries (Burel, 1992; Lys, 1994; Rykken et al., 1997). Many studies have shown that the spatial distributions and dynamics of carabid species are modified by the presence of various kinds of undisturbed areas within agricul-

tural fields. Several hypotheses have been proposed to explain these changes, such as provision of refuge sites in the case of intensive agricultural perturbations (Wallin, 1987), provision of breeding or overwintering areas (Desender, 1982), establishment of corridors for dispersion (Petit and Burel, 1998), and enhancement of prey availability (Zangger, 1994). This work aimed to study how the foraging strategies of the carabid beetle *Pterostichus melanarius* are modified in new field margins habitats.

Several authors hypothesised that in carabids, foraging depends mainly on hunger level (den Boer, 1986; Mols, 1987, 1988). This hypothesis states that displacements are modified by prey intake, and assumes that (1) starved individuals are more active than satiated ones, and (2) this foraging activity is to search for prey. However, experimental studies of foraging in natural conditions remain scarce.

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A capture–recapture experiment was conducted in spring 1997. Beetles whose hunger level was experimentally manipulated (starved or satiated) were released in enclosures covering the field margin habitats. This experiment aimed at answering the following questions: (1) can the relationship between hunger level and foraging activity be observed in the field? (2) If so, what may be the influence of hunger levels on habitat choice?

2. Materials and methods

2.1. Study area

The study area was situated on an experimental farm in the French region of Beauce, an area of intensive arable cropping. On this farm, hedges (maximum height: 2 m) were planted during the winter 1994–1995 (Fournier and Loreau, 1999), and remained totally undisturbed. Four habitats followed each other along a 120 m long gradient (Fig. 1): the hedge *sensu stricto* (habitat H), a mixed crop (habitat MC), and a winter wheat crop (habitat W10 for the first 10 m of the crop, habitat W100 for the centre of the crop).

2.2. Prey availability in the different habitats

Two different methods were employed for evaluating prey availability in the different habitats (for extensive details see Fournier and Loreau, 2001). First, ground-dwelling insects captured in pitfall traps were identified up to the family level, except for Collembola. Second, formaldehyde extractions in soil quadrats (Guillemain et al., 1997), were performed. Four groups of animals were distinguished and weighed (epigeous, anecic and endogeous earthworms, and other prey, except again Collembola). The first method revealed differences in prey diversity among habitats, which was highest in the hedge, lowest in the mixed crop, and low in the cereal crop; the second one also indicated significant variations in prey density and fresh biomass, prey abundance being highest in the hedge (Fournier and Loreau, 2001). This gradient in prey availability seems to be consistent with several other studies (Lewis, 1969; Thomas et al., 1994; Thomas and Marshall, 1999).

2.3. Enclosures

Two rectangular enclosures (length 21 m, width 6.5 m), made of plastic sheets 50 cm high, vertically maintained with stakes and buried in the soil 10 cm deep, were installed in June 1997, 250 m apart. They included three of the four adjacent habitats (H, MC, W10) (Fig. 1). Sixteen pitfall traps were evenly spaced along the interior border of each enclosure (mean distance between two traps: 3.4 m, ± 0.26 S.D.), with one trap at each corner.

2.4. Species studied

P. melanarius Ill. is a nocturnal autumn breeder (Lindroth, 1992), whose size ranges between 12 and 18 mm. It is eurytopic but prefers open habitats, and is rather favoured by agriculture (Desender and Alderweireldt, 1988). As in many carabid beetles, *P. melanarius* has a very unspecific diet (Pollet and Desender, 1985), but synchronises its activity with that of some prey groups such as aphids or slugs (Pollet and Desender, 1987; Symondson, 1997). In a previous study (Fournier and Loreau, 1999) *P. melanarius* was found to be the most abundant species in the study area.

2.5. Rearing of beetles and manipulation of satiation state

Beetles were sampled in the field from 20 May to 10 June 1997. They were placed in individual plastic boxes with a thin layer of soil and a daily moistened filter paper, and fed every 4 days with earthworms, with water given *ad libitum*. Each beetle received an individual mark on its cuticle, using a micro-drill (Loreau, 1984). After 15 days, all beetles were starved for 6 days, with water still given *ad libitum*. After starvation they were weighed to the nearest mg ($W_{B,i}$: the basal body mass of individual *i* after 6 days of starvation). Beetles were then separated into two satiation-state groups: starved and satiated. Satiated individuals were fed with earthworms *ad libitum*. The day after, satiated insects were weighed again ($W_{0,i}$: the initial body mass of individual *i*). Starved individuals were not weighed again just before release, thus $W_{0,i} = W_{B,i}$ for this group. Beetles were released in the centre of each of the three habitat-type areas. The experiment was per-

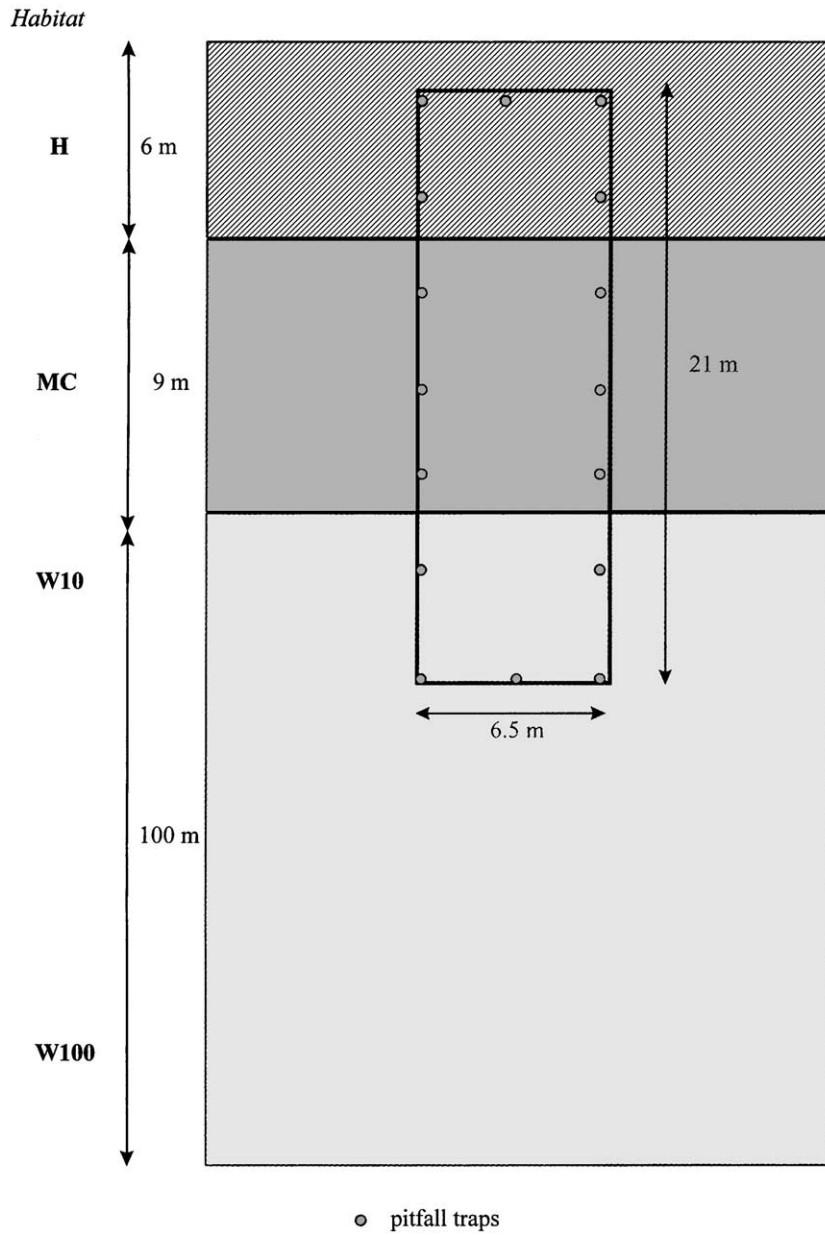


Fig. 1. Enclosure used in the experiment. Habitat types: H: hedge sensu stricto; MC: mixed crop of fodder; W10: edge (first 10 m) of the wheat crop culture; W100: centre of the wheat crop culture (100 m from H).

formed with a total of 127 *P. melanarius* in the starved group and 128 in the satiated group. After release, enclosures were visited every day for 8 days. Each pitfall trap was checked for marked beetles. Recap-

tured individuals were weighed ($W_{d,i}$: the body mass of individual i at day d), then released 20 cm from their trap of recapture to reduce the risk of immediate recapture.

2.6. Measurement of beetle activity

The number of recaptures per individual was first analysed using a non-parametric Kruskal–Wallis test (because of non-normality of data). The mean time of first recapture was also analysed by fitting a logistic regression to the data of first recaptures as a function of date. If N is 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 at day d , k the recapture rate, and R_d the number of newly recaptured individuals at day d , supposing 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 , can be expressed as

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

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

$$R_d = Nk(1-k)^{d-1} \quad (2)$$

where 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, using the NLIN procedure (SAS software). At some dates no individuals were recaptured; these $R_d = 0$ were considered as missing values. The analysis was done for each satiation-state group, both in each enclosure and on the pooled data of both enclosures. Student tests were performed to compare k values using the estimate and asymptotic standard error of k provided by the NLIN procedure.

Table 1

Recapture rates, k , of *P. melanarius*, estimated by logistic regression of the number of newly recaptured individuals as a function of the number of days between release and first recapture^a

Enclosure	Initial satiation state	Number of observations	Estimate of k (number of individuals per day)	Asymptotic standard error of k	Related value of T (day)
E1	ST	6	0.131	0.030	7.640
	SA	7	0.126	0.039	7.928
E2	ST	3	0.160	0.048	6.261
	SA	6	0.121	0.028	8.279
E1 + E2	ST	9	0.141	0.024	7.074
	SA	13	0.124	0.023	8.083

^a The mean time of first recapture is estimated as $T = 1/k$.

2.7. Measurement of beetle body-mass change

The body-mass change between release and first recapture was analysed with the ratio between the body mass at first recapture and the initial body mass: $WR = W_{d,i} / W_{0,i}$. The relationships between body-mass variation and satiation-state group were analysed using contingency tables, with two classes for WR ($WR > 1$: gain of body mass, $WR < 1$ loss of body mass). In this analysis frequencies were summed over both enclosures. Nested ANOVA models were also used to analyse WR as a function of satiation-state group and initial habitat type, but for normalisation of data the variable $1/WR$ was used.

2.8. Displacements of beetles between initial release and first recapture

Displacements between release and first recapture were classified in two “transition groups”: transition type “0” when individuals were recaptured in their initial habitat type, transition type “1” when they were recaptured in another habitat type.

3. Results

3.1. Beetle activity

In each enclosure, the total number of recaptures per individual did not depend significantly on initial satiation state (Kruskal–Wallis non-parametric test: $H = 0.54$, $P = 0.46$, d.f. = 1). Whatever the enclosure, the mean time of first recapture always tended to be lower for starved than for satiated individuals (Table 1). Stu-

dent tests on *k* values were not significant in each enclosure separately (Student test in enclosure E1: $t = 0.24$, $P = 0.41$, d.f. = 11; in enclosure E2: $t = 1.56$, $P = 0.08$, d.f. = 7), but became significant when the logistic regression was fitted to pooled data from the two enclosures ($t = 1.71$, $P = 0.05$, d.f. = 20).

3.2. Beetle body-mass change

The change in body-mass depended significantly on the initial satiation state ($\chi^2 = 29.60$, $P < 0.0001$, d.f. = 1, Table 2). The effect of satiation-state group on body-mass variation between release and first recapture, was significant at least on days 1, 2 and 3 (Fig. 2). Both analyses show that starved individuals gained body mass whereas satiated individuals lost body mass.

Table 2

Effect of initial satiation state on body-mass variation between release and first recapture for *P. melanarius*. Body mass ratios WR were separated in two classes: $WR > 1$ (gain of body mass) and $WR < 1$ (loss of body mass)^a

Weight variation between release and first recapture	Satiation-state group	
	ST	SA
WR < 1	15	50
WR > 1	34	11

^a Frequencies were summed over the two enclosures.

3.3. Beetle displacements

In total 166 recapture events were observed. Insects moved significantly more towards H (57 events in total) or W10 (76 events in total, against 33 towards MC) ($\chi^2 = 16.78$, $P = 0.0002$, d.f. = 2). However, these

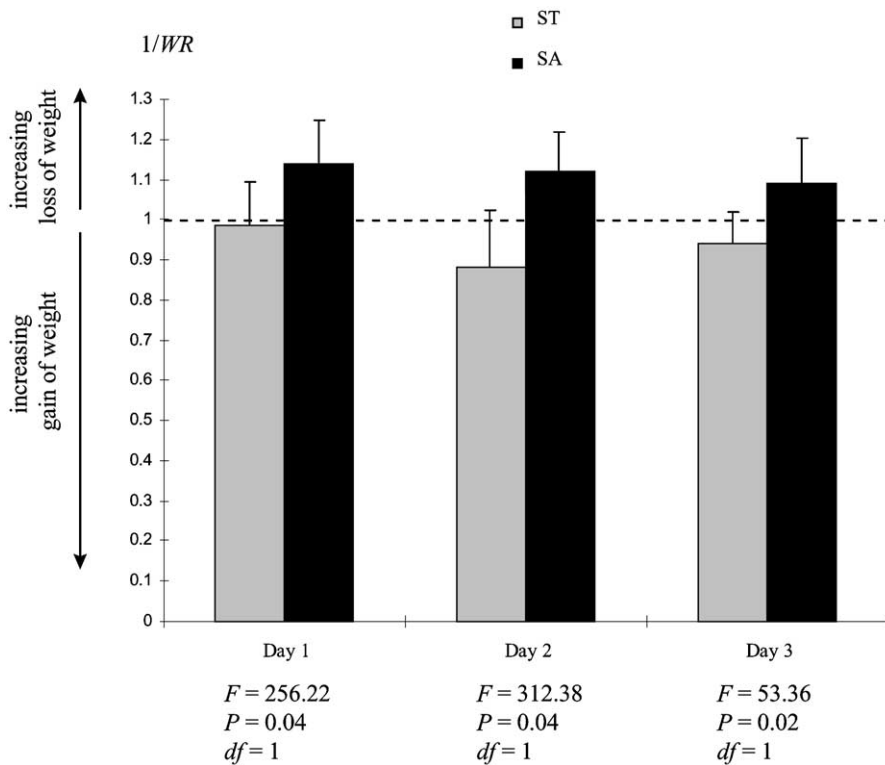


Fig. 2. Effect of initial satiation state on the body-mass variation between release and first recapture for *P. melanarius*. The effect was tested in a nested ANOVA model (effect of satiation-state group nested into effect of enclosure), and data were normalised using an inverse transformation of the variable WR ($WR = W_{d,i}/W_{0,i}$). Analyses were performed separately for each day after release, and for the three dates pooled.

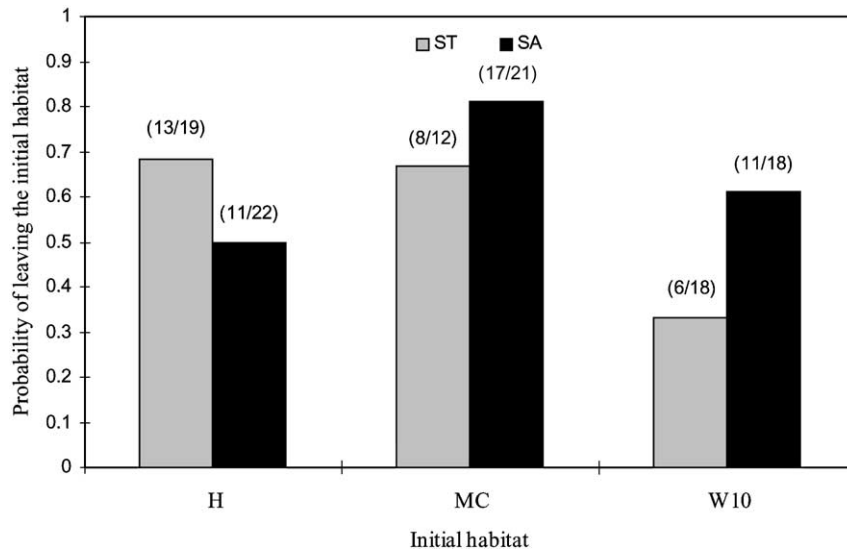


Fig. 3. Probability of leaving the initial habitat between release and first recapture (irrespective of date), for the two satiation-state groups in *P. melanarius*. Frequencies, summed over the two enclosures, are indicated in brackets.

particular directions did not depend significantly on initial satiation state ($\chi^2 = 2.14$, $P = 0.34$, d.f. = 2). The displacements between release and first recapture (all dates of first recapture being included) depended significantly on the interaction between initial satiation state and initial habitat type (Fig. 3): starved individuals that were released in habitat H or MC left their initial habitat significantly more often than those released in W10 ($\chi^2 = 5.86$, $P = 0.05$, d.f. = 2), whereas satiated individuals that were released in H or W10 tended to stay more in their initial habitat than those released in MC (marginally significant trend: $\chi^2 = 4.55$, $P = 0.10$, d.f. = 2).

4. Discussion

Pitfall trapping present several biases: capture rates depend on insect ability to escape from traps, on weather conditions, on vegetation structure, and also there can be border effects. This is not the best methodology for an extensive study of beetles displacements, but for a preliminary experiment it can give interesting results for little investment in time and cost. Also, the experiment was conducted over a limited period and with few replicates. Despite these limitations, it pro-

vided several evidences for the role of satiation state on beetle activity and food intake efficiency in the field for *P. melanarius*. The mean time to first recapture tended to be lower for starved than for satiated individuals, suggesting that the former were more active than the latter. Moreover, the analysis of weight variation between release and first recapture showed that starved individuals gained weight, whereas satiated individuals lost weight. These results are in agreement with the general hypothesis (Grüm, 1971; den Boer, 1986) that foraging mainly depends on hunger level. In particular, Mols (1987, 1988) laboratory and simulation study on *Pterostichus coerulescens* L. suggested that hunger was the main motivation for displacement under controlled conditions. The direction of displacements, analysed on the whole set of recapture events, was not related to the initial satiation state. However, when only first recaptures were considered, the type of displacement occurring between release and first recapture depended significantly on initial satiation state and initial habitat: starved individuals released in H or MC left significantly more often than those released in W10; in contrast satiated individuals released in H tended to stay more in their initial habitat.

These results suggest that *P. melanarius* has a flexible habitat use depending on its initial satiation state

and on the habitat quality: the hedge may be preferred by satiated individuals, whereas this habitat as well as the mixed crop may be avoided by starved individuals, who seem to forage mainly in the cereal crop edge. This is somewhat surprising, because the crop edge is the habitat where prey diversity and biomass are the lowest (Fournier and Loreau, 2001). However, a reduced range of prey might be appreciated by starved *P. melanarius* (Pollet and Desender, 1987; Symondson, 1997). Hence, *P. melanarius* exhibited a flexible habitat use, which might explain its high success in various kinds of habitat.

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