

# EFFECTS OF GRASSY BANKS ON THE DISPERSAL OF SOME CARABID BEETLES (COLEOPTERA: CARABIDAE) ON FARMLAND

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## Abstract

*Mark-recapture experiments in replicated experimental plots were used to assess the relative effects of a barley crop and two widths of a field boundary on the field-to-field movement of three carabid species. Movement of *Harpalus rufipes*, *Pterostichus melanarius* and *P. niger* was slower through a grassy bank than through a barley crop, indicating that the bank had a lower permeability to these species than the crop. Other variables affecting the movement of carabids through the field boundary were species, dietary condition and width of the field boundary. The implications of these results are discussed in relation to the dynamics of carabid dispersal on farmland.*

**Keywords:** field boundaries, dispersal, landscape dynamics, permeability, Norway.

## INTRODUCTION

Dispersal by Carabidae is considered to be important for their long-term survival in agricultural and other fragmented habitats (Southwood, 1962; Den Boer, 1970, 1990; Burkey, 1989; Sherratt & Jepson, 1993). The effectiveness of carabids as natural enemies of crop pests (Luff, 1983; Wratten, 1987; Wratten & Powell, 1991) depends not only upon their ability to penetrate fields from overwintering sites in field boundaries but also on movement on a larger spatial scale, from one field to another. Rates of movement between fields will also affect recovery after population perturbations such as those which may result from pesticide applications (Jepson & Thacker, 1990; Sherratt & Jepson, 1993).

In the mosaic of crop and non-crop habitats comprising an agrarian landscape, movement of some fauna between remnant biotopes is facilitated by the presence

of linear corridors such as hedgerows, grass banks, stone walls, shelter belts and other field boundaries (Baudry, 1988; Dover, 1991; Šustek, 1994). Numerous studies have been published concerning the dispersal of carabid beetles (Den Boer, 1970; Baars, 1979; Rijnsdorp 1980; Coombes & Sotherton, 1986; Wallin, 1986, 1987; Weseloh, 1987; Den Boer, 1990; Duelli *et al.*, 1990; Mader *et al.*, 1990; Loureau & Nolf, 1993; Šustek, 1994; *inter alia*). However, quantification of dispersal between fields requires data on movement across field boundaries. Until the present work was carried out, only one empirical study had examined this aspect of carabid ecology (Duelli *et al.*, 1990). This work showed that almost all species exhibited population exchanges across the borders of a maize field and that the 'edge permeability' of the field depended upon the type of field margin. Hedgerows can impede field-to-field movement in butterflies (Fry & Robson, 1994) and linyphiid spiders (Thomas, 1992), and field boundaries might be expected to reduce or delay dispersal by flightless carabid species.

Studies involving many different organisms have indicated the need to focus on landscape-scale spatial dynamics in agricultural landscapes as a means of obtaining a better understanding of observed temporal and spatial trends in animal distribution and abundance (Fry, 1994). Examples on farmland of the effects of landscape pattern on population processes include birds (Opdam, 1990; Rolstad, 1991), amphibians (Sjögren, 1991) and mammals (Verboom *et al.*, 1991). In the mosaic of habitats which form an agricultural landscape it may be appropriate to view landscape-scale carabid assemblages as metapopulations which comprise a system of populations inter-linked by dispersing individuals and in a balance between local extinction and recolonisation (Gilpin & Hanski, 1991; Sherratt &

Jepson, 1993; Booij & den Nijs, 1992). Dispersal at the landscape scale has been considered important in determining species' vulnerability to pesticides (Burn, 1992; Jepson, 1993; Sherratt & Jepson, 1993), their sensitivity to farming operations (Booij & den Nijs, 1994) and in determining long-term biogeographic trends (Hengeveld, 1985). Information on the permeability of linear features and its effects on carabid dispersal would be of considerable value for the refinement of spatially explicit population models (e.g. Hanski & Thomas, 1994) and as an aid to carabid conservation.

This study set out to investigate if a grassy bank, a common type of field boundary throughout north-western Europe, influenced movement of carabids between cereal fields. The specific aims of the study were to determine: (1) if the presence of a grassy bank affected rates of movement of carabids; (2) if there was a relationship between rates of movement and bank width; (3) whether different species responded in the same way to a grassy bank; and (4) the effect of a grassy bank on the movement of hungry and satiated carabids. The latter investigation was conducted because differences in the activity of hungry and satiated carabids (Lenski, 1984) could affect their response to a field boundary.

## MATERIALS AND METHODS

### Study site

The field boundary was a 176 m-long north-south grassy bank between a 33-ha field of spring barley cv. Gunilla and a 0.8-ha field of spring oats cv. Mustang; it separated two farms 25 km south of Oslo, Norway. The soil type in both fields was a light clay, with patches of fluvial silt deposits in the barley field. No fungicides, herbicides or insecticides were applied to either crop for the duration of the study.

The experimental grassy bank had a mean width of 1.32 m and a height of 0.26 m above the barley field. Ground vegetation had a mean height of 0.23 m above the soil bank and dead inflorescences of *Anthriscus sylvestris* (L.) Hoffm. reached a mean height of 0.82 m above the bank. On the barley side, the bank had a vertical face of mean height 0.15 m and was separated from the crop by a strip of bare soil and weeds (mean width 0.16 m). During the third week of July, estimates were made of the plant species cover in the grassy bank and in the adjacent strip. The predominant species in the bank were *A. sylvestris* (47% ground cover) and *Elymus repens* (L.) Gould (32%). Ground cover in the strip was mostly *Viola arvensis* Murray (43%) and exposed soil (42%). In the barley crop within the experimental plots, the mean density of barley stems was 992 m<sup>-2</sup> (equivalent to about 65% ground cover) and weeds had 11% ground cover.

### Experimental plots

The experimental design comprised 15 plots of 2.3 m × 4 m plots situated along the most uniform (78 m) section of the bank and included three boundary comparisons ('treatments'), each replicated five times in a randomised

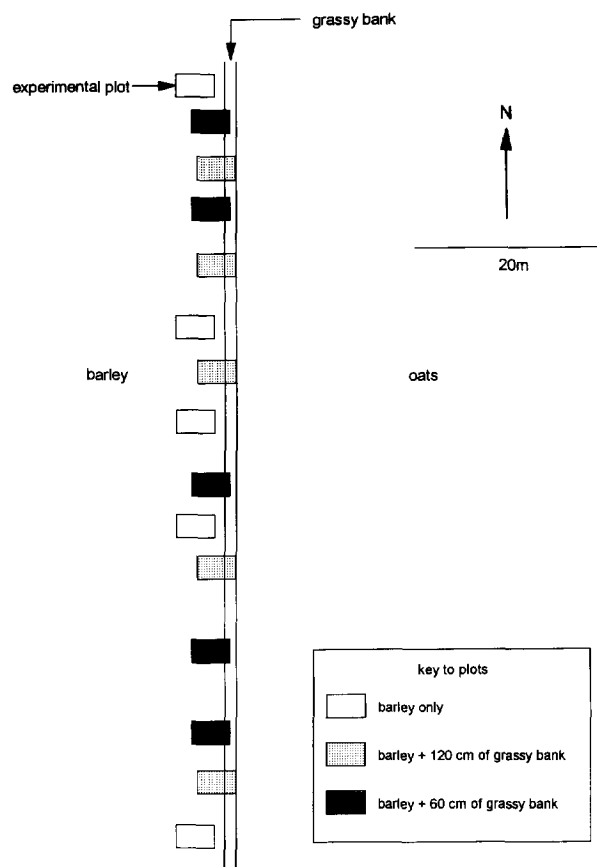


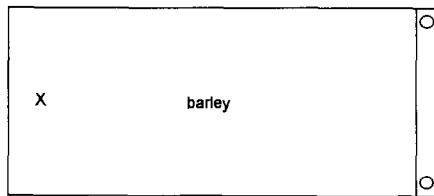
Fig. 1. The layout of the experimental plots.

block design (Fig. 1). The treatments were: (1) barley crop alone; (2) barley plus a 0.6 m width of grassy bank; and (3) barley plus a 1.2 m width of bank (Fig. 2). Treatments were enclosed by polythene barriers on three sides and on the end nearest or in the bank by a gutter trap sunk 5 cm into the ground. This design was to maximise recapture of marked carabids, which can be very low in an unenclosed area. For instance, Coombes and Sotherton (1986) recovered only 0.4%–2% of the marked *Agonum dorsale* they released into field boundaries. The polythene barriers extended c. 20 cm below the soil surface in the barley field and c. 40 cm above it. The plots were set up at the end of June and traps were provided with lids of inverted guttering supported on wire stays to prevent predation by birds. Small plastic beakers containing stones and moistened peat for shelter were placed in the downpipes at the end of each gutter trap to collect live carabids (Fig. 2).

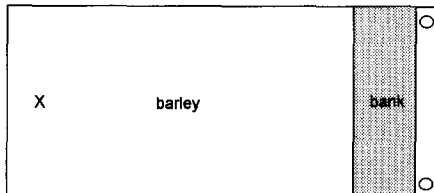
### Choice and maintenance of test species

Three species of Carabidae were used in this study: *Harpalus rufipes* (Degeer), *Pterostichus melanarius* (Illiger) and *P. niger* (Schaller). These species were chosen because they are among the most abundant Carabidae found in summer as adults in arable and other crops throughout north-west Europe (Turin *et al.*, 1977), they are large species which are easy to handle and mark and they represent an important group of polyphagous predators of arable crop pests (Wratten & Powell, 1991).

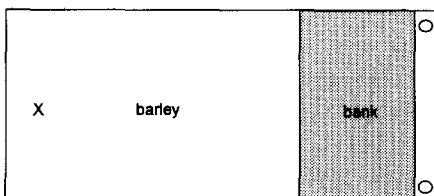
## 1. Barley only



## 2. Barley with 60 cm-wide grassy bank



## 3. Barley with 120 cm-wide grassy bank



← 4m →

Fig. 2. The three types of experimental plot used in mark-recapture experiments. Carabids were released at a standard position (X) and recaptured in plastic beakers (O) set in gutter traps at the opposite end of the plot. Each type of plot was replicated five times (see Fig. 1).

Individuals were collected in 1.5 m-long dry gutter traps placed in arable fields up to 5 km from the study site. Subsequently, the catches were maintained in a 'Convion' constant environment room at a temperature of  $15.0 \pm 0.5^\circ\text{C}$  and a relative humidity of  $90 \pm 1.0\%$ . The light regime was 18 h light: 4 h dark separated by two 1-h periods of 50% illumination to mimic the mid-summer daylength in southern Scandinavia. Carabid species were kept separately in 32 cm  $\times$  26 cm  $\times$  20 cm white plastic crates provided with a c. 10-cm layer of garden peat and had *ad lib.* access to food and water

except for specific starvation experiments when food was withheld for at least five days prior to release (Table 1). Food consisted of moistened, crushed, dry dog meal placed in inverted lids of two 7 cm-diameter perspex Petri dishes per crate and was replaced at least every 48 h. Water was provided in two saturated wads of cotton wool in each crate, also in inverted Petri dish lids, and these were replenished every 24 h. Carabid densities per crate varied up to a maximum of c. 200 but for at least 48 h prior to their release in field experiments the beetles were kept at maximum densities of 100 per crate. At these densities cannibalism was almost eliminated but a few incidents were observed, especially with *P. melanarius*.

### Marking

A number of methods have been used for marking the elytra of carabids including puncturing (e.g. Weseloh, 1987), scratching (e.g. Wallin, 1986), grinding (e.g. Loreau & Nolf, 1993), branding (e.g. Rijnsdorp, 1980), breaking (e.g. Coombes & Sotherton, 1986), ink marking (e.g. Lys & Nentwig, 1991) and painting (e.g. Lawrence & Bach, 1989). Paint-marking the insects was used in this study for two reasons: (1) large numbers of insects can be marked quickly; (2) different cohorts can easily be distinguished at a glance in the field by using contrasting colours. This is a suitable method provided that the possibility of paint wear during an experiment is taken into account when interpreting the results (e.g. Lawrence & Bach, 1989). A laboratory experiment to examine paint wear under controlled conditions over an 8-day period showed that loss of marks differed between species but was not affected by dietary state or paint colour: overall, a mean of 70% of *P. melanarius* and 100% of *H. rufipes* retained marks of 'Revell' enamel modellers' paint (Revell AG, Bünde, Germany). Interpretation of the results of recapture experiments takes these differences into consideration.

### Calabid release and recapture

Six release-recapture experiments were conducted in July–August 1992 when the carabid beetles used in this study are at their peak activity searching for food and breeding in cereal crops. Details are given in Table 1.

Table 1. Details of release-recapture experiments, summer 1992

| Experiment | Species              | Diet    | Days of contrast in diet before insects released | Released |            | Number released per plot | Experiment duration (days) |
|------------|----------------------|---------|--------------------------------------------------|----------|------------|--------------------------|----------------------------|
|            |                      |         |                                                  | Date     | Time (GMT) |                          |                            |
| 1          | <i>P. melanarius</i> | Fed     | —                                                | 5 July   | 2150 h     | 100                      | 29                         |
| 2          | <i>H. rufipes</i>    | Fed     | —                                                | 6 July   | 2100 h     | 100                      | 28                         |
| 3          | <i>P. melanarius</i> | Fed     | —                                                | 15 July  | 2215 h     | 100                      | 18                         |
|            | <i>P. niger</i>      | Fed     | —                                                | 15 July  | 2215 h     | 27                       | 18                         |
| 4          | <i>P. melanarius</i> | Fed     | 7                                                | 20 July  | 2245 h     | 44                       | 13                         |
|            |                      | Starved | 7                                                | 20 July  | 2245 h     | 44                       | 13                         |
|            | <i>H. rufipes</i>    | Fed     | 7                                                | 20 July  | 2245 h     | 44                       | 13                         |
|            |                      | Starved | 7                                                | 20 July  | 2245 h     | 44                       | 13                         |
| 5          | <i>P. melanarius</i> | Fed     | —                                                | 25 July  | 0045 h     | 50                       | 9                          |
|            | <i>P. niger</i>      | Fed     | —                                                | 25 July  | 0045 h     | 28                       | 9                          |
| 6          | <i>P. melanarius</i> | Fed     | 9                                                | 26 July  | 2230 h     | 46                       | 7                          |
|            |                      | Starved | 9                                                | 26 July  | 2230 h     | 46                       | 7                          |

All carabid releases were carried out at night (between 2100 h and 0100 h GMT) (cf. Wallin, 1986) as this is when the three species are most active in the field (Luff, 1978); release during the day would have caused relatively more disturbance to the carabids and increased the chance of predation by birds. At least 48 h prior to release into the experimental plots, each cohort (species or diet group) of carabids was randomly divided up and placed in 15 plastic crates; these were maintained under the controlled laboratory conditions described above. At the start of a release experiment, each crate of beetles was randomly assigned to one of the 15 experimental plots and in all plots simultaneously the carabids and peat were tipped out onto the soil at 1.0 m from the field end of the plot.

Recaptures of marked carabids were recorded in the gutter traps at daily intervals after their release. Traps were checked in the morning between 0700 and 0900 h GMT. Checks made at midday and in the afternoon indicated that very few marked carabids were active after 0900 h GMT. Traps were reset periodically, especially after rain, to ensure that their capture efficiency did not differ markedly between plots or days.

#### Analysis of recapture data

For each experiment, recapture data were expressed as the accumulated percentage of the marked population that was recaptured each day after release. Recapture curves were used to interpolate mathematically the number of days,  $x$ , for a given proportion,  $y$  (25%, 50% or 60%), of the marked population to be recaptured, so that  $x$  could be compared for different treatments, species or dietary states (Table 2). These curves were fitted to the arcsine-transformed accumulated recapture data using non-linear least-squares regression. Two- or three-parameter quadratic curves were used to obtain a good description of the data ( $R^2 > 0.9$ ) in all experi-

ments. Effects of different treatments, species or their dietary condition on recapture times were examined by comparing derived recapture curves and the recapture times interpolated from them (Figs 3–5 show examples). One-way (boundary treatment), two-way (treatment and species) or three-way (treatment, species and diet) analyses of variance on interpolated recapture times were used to identify differences in recapture times which could be explained by the variables treatment, species or diet.

## RESULTS

Comparisons of boundary treatment, species and diet made during six mark-recapture experiments are given in Table 1. Mathematically interpolated recapture times (days) for recapture of 25% and 50% of marked carabids are given in Table 2. Some shorter experiments did not achieve recaptures of 50%, whilst in others, recapture success was very high; 100% of marked carabids were recaptured in some plots in Experiments 1 and 3. There was a clear difference between species in the retention of paint marks, with virtually no loss of paint from the pubescent elytra of *H. rufipes* whereas up to 30% of *P. melanarius*, which have glabrous elytra, had lost marks. There was, however, no evidence for an effect of dietary condition on the wear of paint marks, as might be expected if differences in diet cause differences in carabid activity (e.g. Lenski, 1984). Paint wear was not examined separately for *P. niger* because the elytral cuticles of both *Pterostichus* spp. are morphologically similar.

#### Effects of the grassy bank on capture rate

Both widths of the grassy bank slowed recapture of all three species relative to the barley crop (Table 2). In all experiments the difference in recapture rate between the

Table 2. Mean number of days elapsed for recapture of 25% and 50% of the marked population

| Experiment | Species              | Diet    | Reference recapture | Time taken (days $\pm$ one standard error) <sup>a</sup> |                          |                          |
|------------|----------------------|---------|---------------------|---------------------------------------------------------|--------------------------|--------------------------|
|            |                      |         |                     | Barley crop                                             | Barley + 0.6 m-wide bank | Barley + 1.2 m-wide bank |
| 1          | <i>P. melanarius</i> | Fed     | 25%                 | 1.3 $\pm$ 0.2                                           | 1.6 $\pm$ 0.1            | 1.6 $\pm$ 0.2            |
|            |                      |         | 50%                 | 2.6 $\pm$ 0.5                                           | 3.1 $\pm$ 0.3            | 3.1 $\pm$ 0.4            |
| 2          | <i>H. rufipes</i>    | Fed     | 25%                 | 0.8 $\pm$ 0.1                                           | 1.4 $\pm$ 0.1            | 1.7 $\pm$ 0.2            |
|            |                      |         | 50%                 | 1.7 $\pm$ 0.3                                           | 3.1 $\pm$ 0.4            | 4.5 $\pm$ 0.9            |
| 3          | <i>P. melanarius</i> | Fed     | 25%                 | 0.7 $\pm$ 0.1                                           | 0.9 $\pm$ 0.1            | 1.1 $\pm$ 0.2            |
|            |                      |         | 50%                 | 1.3 $\pm$ 0.1                                           | 1.7 $\pm$ 0.1            | 2.2 $\pm$ 0.4            |
| 4          | <i>P. niger</i>      | Fed     | 25%                 | 0.8 $\pm$ 0.1                                           | no data                  | 1.0 $\pm$ 0.2            |
|            | <i>P. melanarius</i> | Fed     | 25%                 | 0.6 $\pm$ 0.2                                           | 1.4 $\pm$ 0.4            | 1.3 $\pm$ 0.2            |
|            |                      | Starved | 25%                 | 0.5 $\pm$ 0.2                                           | 0.9 $\pm$ 0.2            | 0.9 $\pm$ 0.3            |
|            |                      |         | 50%                 | 1.1 $\pm$ 0.5                                           | *                        | 2.1 $\pm$ 0.4            |
|            | <i>H. rufipes</i>    | Fed     | 25%                 | 0.5 $\pm$ 0.1                                           | 1.1 $\pm$ 0.2            | 1.1 $\pm$ 0.2            |
|            |                      | Starved | 25%                 | 1.1 $\pm$ 0.3                                           | 2.5 $\pm$ 1.5            | *                        |
| 5          | <i>P. melanarius</i> | Fed     | 25%                 | 2.7 $\pm$ 0.4                                           | 3.9 $\pm$ 0.4            | 3.3 $\pm$ 0.2            |
|            | <i>P. niger</i>      | Fed     | 25%                 | 3.6 $\pm$ 2.3                                           | 4.1 $\pm$ 2.8            | *                        |
| 6          | <i>P. melanarius</i> | Fed     | 25%                 | 2.7 $\pm$ 0.6                                           | 4.0 $\pm$ 0.9            | 3.5 $\pm$ 0.3            |
|            |                      | Starved | 25%                 | 0.9 $\pm$ 0.2                                           | 1.3 $\pm$ 0.1            | 1.5 $\pm$ 0.3            |
|            |                      |         | 50%                 | 2.6 $\pm$ 0.4                                           | 3.5 $\pm$ 0.6            | 3.6 $\pm$ 0.6            |

<sup>a</sup>Asterisks indicate that the time taken to reach a specified percentage recapture exceeded the duration of the experiment.

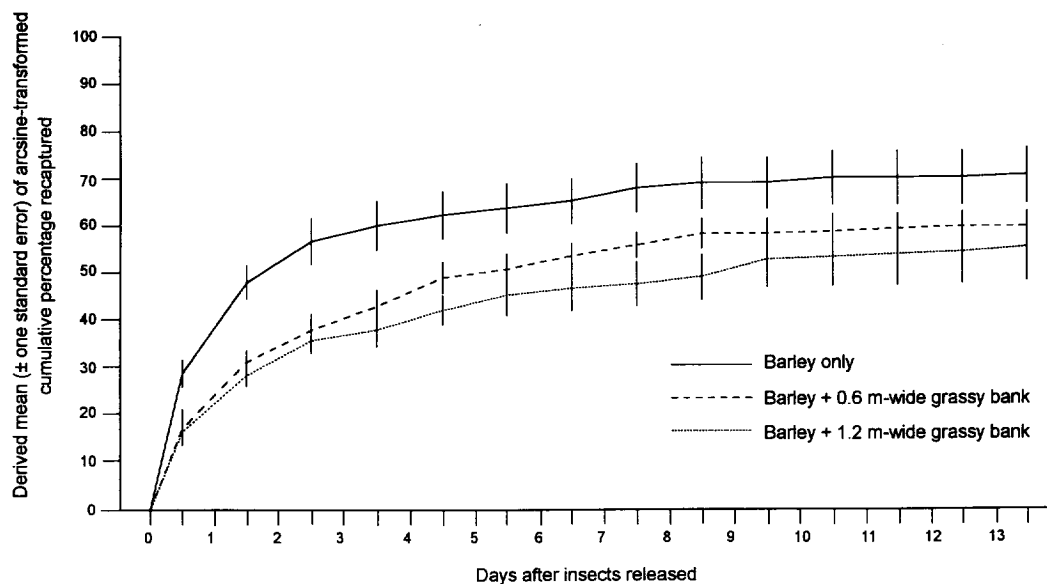


Fig. 3. Effect of different widths of grassy bank on recapture of *Harpalus rufipes* in Experiment 4.

barley crop and the grassy bank was greater than the difference between the two widths of bank. In some cases there was little difference between the 0.6 m and 1.2 m widths of the bank (Table 2) but where there were large differences, the wider bank generally had the greater slowing effect on recapture (Fig. 3). Statistical analyses of variation in recapture times between the barley crop and the wide grassy bank (one-way analysis of variance followed by Tukey's multiple range test) revealed significant differences ( $p < 0.05$ ) for recapture of 25% and 60% of *P. melanarius* in Experiment 3 and for 25% recapture ( $p < 0.01$ ) and 50% recapture ( $p < 0.05$ ) of *H. rufipes* in Experiment 2; none of the other comparisons was statistically significant ( $p > 0.05$ ).

#### Effect of diet

The effect of diet on carabid movement was examined by comparing recapture rates of starved and fed cohorts of *H. rufipes* and *P. melanarius* (Tables 1 and 2).

Starved *P. melanarius* in two experiments were consistently recaptured more quickly than the fed cohort (Fig. 4; Table 2). Differences in the times taken to recapture 25% of the starved and fed insects were significant in Experiment 6 ( $p < 0.001$ ) but not in Experiment 4 ( $p > 0.05$ ). The results from one experiment with *H. rufipes* show that starved beetles were recaptured more slowly than the fed cohort (Table 2) but these differences were not significant ( $p > 0.05$ ). For both species the time difference between recaptures of starved and fed cohorts was increased by the presence of the grassy bank (Table 2).

#### Comparison of species

Recaptures were compared for *H. rufipes* and *P. melanarius* in Experiment 4 and for *P. melanarius* and *P. niger* in Experiments 3 and 5 (Table 1).

Overall, the starved cohort of *P. melanarius* was recaptured more quickly than the starved cohort of

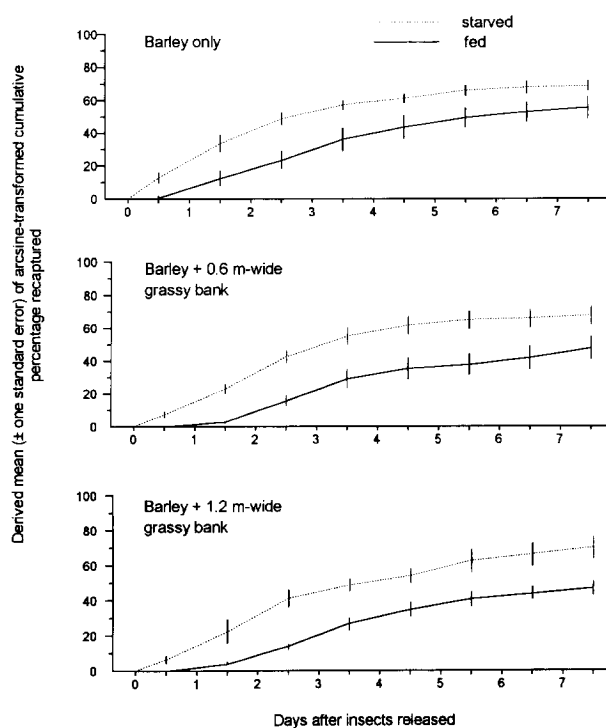


Fig. 4. Effect of diet on recapture of starved and fed *Pterostichus melanarius* in Experiment 6.

*H. rufipes* and this difference between species was increased by the presence of the grassy bank (Fig. 5; Table 2). This difference may have been underestimated if, as laboratory results suggested, up to 30% of *P. melanarius* had lost their paint marks. In contrast, there was no clear difference in recaptures of these species when the fed cohorts were compared (Table 2); this reflects differences between the species in the effects of diet (described above). As with the starved cohorts, it is possible that some loss of paint marks from *P. melanarius* could have obscured a higher recapture rate for *P. melanarius* than

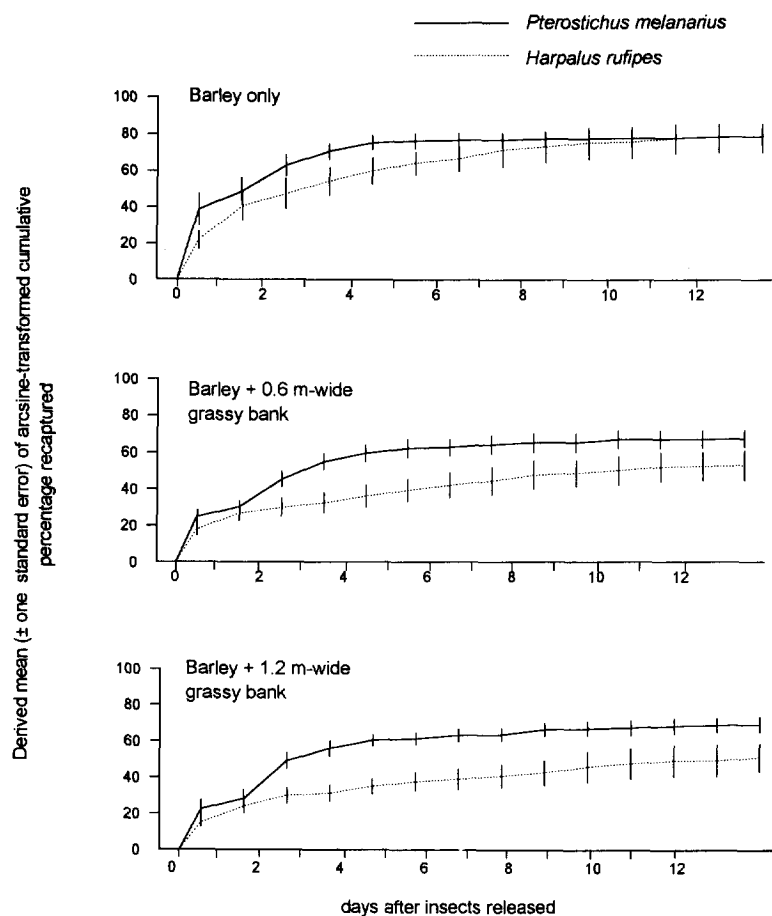


Fig. 5. Comparison of recaptures of starved *Harpalus rufipes* and *Pterostichus melanarius* in Experiment 4.

for *H. rufipes*. However, paint wear in the laboratory was shown to be unaffected by dietary state, so it is valid to make relative comparisons between the recapture rates of the starved and fed cohorts. There was no clear difference between the recapture rates of *P. melanarius* and *P. niger* in Experiment 3 but in Experiment 5, *P. melanarius* was recaptured more quickly. However, relatively small numbers of *P. niger* were used in these experiments, and standard errors were large (Table 2).

## DISCUSSION

The concept of permeability is now accepted as a means of describing the way landscape features such as crops and field boundaries influence the rate of movement of fauna (Sherratt & Jepson, 1993; Fry, 1994; Jepson, 1994) and has been used in studies addressing the conservation of populations in farmland (Fry, 1994). Landscape permeability depends not only upon properties of the landscape, but also upon the behaviour of the fauna and would be expected to differ between species, particularly those with markedly differing dispersal abilities. To date much of the work investigating the permeability of landscape features has been theoretical (Kareiva, 1990; Jepson, 1994). Our study has provided empirical data on the effect of a grassy bank on the rate of movement of large species of Carabidae in farmland. The study was conducted at

one location in Norway using one type of field boundary, but subsequent work in the UK indicates that similar results can occur elsewhere with other types of field boundary (Mauremootoo & Wratten, 1994). However, it would be unwise to generalise the results of our study in summer to other times of year because seasonal changes which occur in the vegetational structure of the landscape (Lys & Nentwig, 1991) and in the demography, foraging and reproductive behaviour of carabid populations (Luff, 1987) would be expected to affect landscape permeability. In our work microclimatic differences between the grassy bank and crop were observed to vary temporally within the duration of the study. For example, the overnight (2200–0500 h GMT) soil surface relative humidity was similar in the bank and crop up to mid-July, but in late July and August was up to 5% lower in the crop than in the bank.

Our study set out to measure the relative permeability of a grassy bank and cereal crop to carabids and showed that the bank had a lower permeability than the crop to all three study species. The causal mechanisms resulting in the observed lower permeability of the grassy bank for carabid movement were not investigated but may have included: (1) changes in speed and/or directionality of movement in response to the microclimatic conditions of the bank or the density of vegetation (Lys & Nentwig, 1991; Šustek, 1994; Vermeulen, 1994); (2) relatively high prey availability in

the bank (Speight & Lawton, 1976); (3) differences in carabid burrowing behaviour between the crop and the bank (Wallin & Ekbom, 1988); (4) the physical structure of the grassy bank habitat causing, for example, avoidance of the bank by carabids because of a steeply sloping face; and (5) the presence of a bare soil strip between the barley crop and the bank. It was not clear which of these was the most important factor impeding carabid movement. Measurements showed that the overnight mean soil surface temperature (2200–0500 h GMT) was consistently higher in the bank than in the crop, the largest difference being c. 2°C, on 25–26 July. Observations also showed that some individuals of each species crossed the bare soil strip and climbed the vertical face of the bank within 1 h of their release. There is experimental evidence from other studies that other Coleoptera may move parallel to crop edges instead of through them (Bohlen & Barrett, 1990). Even within a cereal crop, rows of wheat plants have been found to affect the movement patterns of *H. rufipes*, *P. melanarius* and *P. niger* (Lys & Nentwig, 1991).

The results of these experiments show that the grassy bank was less permeable than an equal width of the barley crop and would reduce the field-to-field movement of *Harpalus rufipes* and *Pterostichus melanarius* in summer. There was also evidence for a similar effect with *P. niger*, although relatively small numbers of this species were available for this study. In some experiments the permeability of the grassy bank clearly decreased with an increase in bank width (Fig. 3) but overall there was no evidence for a direct relationship between the width of the bank and its permeability to these carabids. Hunger was an important factor influencing the different permeability of the bank to *P. melanarius* and *H. rufipes*; starved *P. melanarius* were recaptured more quickly than fed cohorts but it was rather the reverse for *H. rufipes*, with the result that differences in the recapture rates of these two species were only clearly evident when the starved cohorts (Fig. 5) were compared. The reasons for the inconsistent responses of these species to starvation were not clear. It is possible that our starvation method might have been more effective for one of the species than the other (e.g. some cannibalism was observed with *P. melanarius* during the starvation period). Differences in overall rates of movement between hungry and satiated cohorts of these species were not detected by Wallin and Ekbom (1988) using a radar-tracking method over a larger spatial scale. Recaptures of the fed cohorts of *P. melanarius* and *P. niger* suggest that the former moved faster but clear distinctions were precluded by the small numbers of *P. niger* available.

Initial recaptures allowed an estimate of the rate of movement of *P. melanarius* to be made at the time of their release. Some specimens of this species were trapped within 20 min of release, giving a rate of c. 0.2 m min<sup>-1</sup> (9 m h<sup>-1</sup>), assuming a direct path was taken. This is within the range observed for this species at night by Wallin and Ekbom (1988) (0.3–17.0 m h<sup>-1</sup>) but it appears to exceed the range observed by Lys and

Nentwig (1991), although the latter work did not state whether the 'daily' distances moved by carabids referred to 12 or 24 h periods. Considerable between-studies variation in observed rates of movement is to be expected because many factors may affect carabid activity (Luff, 1987), including the design and execution of an experiment. In the present work, carabid movement may have been accelerated by the encounter and subsequent following of the surrounding polythene barriers. Observations confirmed that some individuals of all three species did follow edges, but others entered the traps away from the barriers. The long recapture times in some experiments (asterisks in Table 2 show where recapture times exceeded the duration of experiments) also confirm that edge-following was not a major problem but may have led to an over-estimation of the natural speed of crossing a grassy bank.

Not only do field boundaries provide shelter, a place to breed and overwinter (Thomas *et al.*, 1991, 1992; Dennis *et al.*, 1994; Wratten *et al.*, 1995) but enclosure of sub-populations in fields surrounded by boundaries may partially protect them from the consequences of pesticide use, cultivations at a crucial time in the phenology or random catastrophic events that may deplete other neighbouring sub-populations (Kareiva, 1990). On the other hand field boundaries should be sufficiently permeable to permit colonisation of new habitats or recolonisation of depleted ones. Thus it seems that field boundaries can have both positive and negative consequences for beneficial arthropods but the degree to which they are an asset or a liability is not yet clear and could vary through the year as the relative importance of their different roles changes.

The ability of landscape features such as grassy banks and hedgerows to limit field-to-field dispersal of Carabidae raises questions concerning the landscape dynamics of these beneficial insects on farmland. Such questions are being addressed by theoretical modelling (Kareiva, 1990; Sherratt & Jepson, 1993; Jepson, 1994) but such models have had to assume movement rates for 'generalised' carabids and rely on hypothetical landscape data. Recent simulation modelling has shown that the probability of local carabid populations persisting is influenced by a number of variables, including the permeability of field boundaries (Sherratt & Jepson, 1993). Our empirical data will allow such models to be refined and tested.

This work has shown consistent differences between a barley crop and a grassy bank in their effects on carabid movement. The species used are among the largest (1–2 cm in length) and most mobile of those European carabids which do not fly regularly and it is probable that other species with poorer dispersal abilities (e.g. small species without functional wings) would be affected more strongly by field boundaries. For example, the small (c. 0.4 cm-long) carabid *Bembidion obtusum* Serville would be expected to respond to the physical structure of the grassy bank habitat differently from those species studied in our experiments. Manipulation of landscapes could have important consequences for

carabid populations by affecting the availability and quality of refugia (Coombes & Sotherton, 1986; Thomas *et al.*, 1991, 1992; Dennis *et al.*, 1994; Wratten *et al.*, 1995). Our results suggest that such landscape manipulation could also have important consequences for carabid populations by affecting their rates of dispersal. Farmland can be manipulated in a positive way to conserve both a high diversity of carabids (Fry, 1994) and those important for effective pest control (Thomas *et al.*, 1991, 1992). Such work should integrate knowledge on the role of field boundaries as refuges for beneficial arthropods with that on their impact on local movement and large-scale dispersal to develop management guidelines for both conservation and agricultural goals.

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