Oecologia (1998) 116:103–112 © Springer-Verlag 1998

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Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland

Received: 26 January 1998 / Accepted: 1 April 1998

Abstract The activity and density of the carabid beetle, *Pterostichus melanarius*, were studied over 10 weeks in a continuous mark-recapture experiment using a grid of pitfall traps spanning a hedgerow and extending approximately 30 m into two cereal fields; 1777 beetles were individually marked. The recapture rate was approximately 60% and 40% for males and females, respectively. Activity-density rose and fell four times between early June and mid August. Jolly-Seber estimates of density showed population density increasing to a single peak in late July. The mean population density in late July and August was relatively stable at approximately 0.26 m^{-2}. Activity varied over the 10 weeks and was significantly higher during August than in June or July. The daily displacement distance frequencies, calculated from 750 male and 485 female recaptures of individually marked beetles, were distributed exponentially. Mean displacement distances were approximately 2.6 m day^{-1} during June and July, and 5.3 m day^{-1} during August. A diffusion model provided diffusion coefficients of 23.7 and 27.9 m^2 day^{-1} for female and male beetles, respectively. The spatial distribution of *P. melanarius* was aggregated in patches. Spatial analysis by distance indices showed the spatial distribution of counts between successive periods of activity-density to be significantly associated. Approximately 5.75% of recaptures were from releases on the opposite side of the hedgerow. Approximately 20% of recaptures were from releases in opposite halves of the grid within the same field. The hedgerow acted as a significant barrier to dispersal between fields, with implications for the metapopulation structure of the species.

Key words Dispersal · Mark-recapture · Metapopulation · Pitfall trap · Population density

Introduction

Carabid beetles are commonly studied in agricultural ecosystems because of their importance as predators of pests (Sunderland 1975), as a component of invertebrate food in the diet of birds (Lindroth 1992), especially chicks (Evans 1997; Potts 1997) and because they form a major part of the overall biodiversity found in seminatural habitats on farmland (Burel and Baudry 1995). In the majority of cases, the standard sampling method for carabid populations is the pitfall trap. It is widely recognised that pitfall trap catches depend on both population density and an organism's activity, to provide a quantity usually referred to as activity-density. The interpretation of pitfall trap data to derive an estimate of carabid population density is therefore often complicated and potentially subjective, since analyses of effects normally rely on comparisons of activity-density, assuming activity to be similar in all treatments or habitats. However, while adult population density is generally assumed to change relatively slowly within a season, unless highly disruptive treatments are used which affect mortality, a number of factors can affect intrinsic and apparent activity over short time-scales. Circadian rhythms of activity can be disturbed by sublethal doses of pesticides (Kennedy et al. 1997). Activity can change in response to temperature (Honek 1997), prey density, hunger level or reproductive state (Wallin and Ekbom 1994). In terms of the probability of encountering a trap, apparent activity can also be influenced by factors such as soil microtopography (e.g. smooth, rough or deeply fissured soil surfaces), vegetation structure and vegetation density (Greenslade 1964a; Honek 1988).

The shortcomings of pitfall traps have led to the use of other sampling methods to estimate carabid population density, for example, removal sampling (Baars 1979; Clark et al. 1995), barriered pitfalls (Desender and Maelfait 1986), quadrat sampling (Andersen 1995), emergence traps (Helenius 1995; Purvis and Fadl 1996),

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litter-washing and Tullgren extraction (Spence and Niemela 1994). These methods, however, often necessitate limited sample size and small spatial scales. When pitfall trapping is combined with mark-recapture methods, absolute estimates of population density can be made (Ericson 1977).

Quantifying invertebrate activity is also important because of its relevance to habitat selection (Evans 1983), aggregation of predators in areas of high prey or plant density (Speight and Lawton 1976), recolonisation of fields following pesticide application (Thomas et al. 1990) and in the interaction between local populations in metapopulation dynamics (Sherrat and Jepson 1993). Carabid dispersal has been quantified directly by radar tracking individual beetles (Wallin and Ekbom 1988, 1994). While these methods provide details of an individual's movements (although the effect of diode tags and antennae on their behavior is unknown), pitfall trap studies combined with mark-recapture techniques can provide information on carabid dispersal at the population level (Lys et al. 1994).

In the present paper, we report the results of a large-scale mark-recapture experiment designed to isolate the components of activity and density in pitfall data, by frequent sampling of the carabid beetle, *Pterostichus melanarius* (Ill.), in a high-density grid of pitfall traps in cereal fields. *P. melanarius* is a large carabid suitable for marking. It is one of the most abundant carabids in arable systems and is widespread throughout Europe and Fennoscandia (Lindroth 1992) and has been introduced into Canada and the USA. It is a nocturnally active species of potential economic importance as a predator of aphids (Sunderland 1975) and slugs (Symondson et al. 1996). We present activity-density data over a period of 10 weeks and calculate absolute density from mark-recapture data to infer relative changes in activity. Overall differences in the activity of male and female beetles are compared in terms of a frequency distribution of recapture rates, mean daily displacements and a diffusion process. Distances and times between recaptures are used to demonstrate the scale of dispersal and to quantify changes in activity over time. Recapture data are also used to show the effect of a field boundary on movement between fields. Finally, a recently introduced analytical procedure for spatial data, termed SADIE (spatial analysis by distance indices) (Perry 1995, 1998a,b,c; Korie et al. unpublished) is used to analyse the stability of the two-dimensional pattern of aggregation over time. The spatial stability of the activity-density distribution pattern is discussed in relation to the observed mobility of the beetle.

Materials and methods

The field site was situated at Long Ashton Research Station in the west of England (OS grid reference: ST537693) on a heavy clay soil and comprised two adjacent fields of winter barley, each approximately 3.4 ha, separated by a hedgerow/shelter-belt, 5.3 m wide and 120 m long, oriented north-south. The ground flora of the hedgerow was dominated by ivy (*Hedera helix*) on a slightly raised bank with a shrub layer and a number of mature trees. On the east side of the hedgerow, a 4-m-wide experimentally sown field margin had been established in the previous year, comprising three replicate blocks of four 10-m plots sown with *Lolium perenne*, mixed grasses and wild flowers, natural regeneration or winter barley, arranged randomly within the blocks.

The beetles were sampled with pitfall traps (plastic cups diameter 60 mm, depth 70 mm, with snap-on lids), each set in a plastic sleeve flush with the soil surface. The traps were arranged in a 12×13 grid at 10-m intervals along the north-south axis, and at 5.3-m intervals along the east-west axis (scaled to the width of the hedgerow), such that six columns of traps were to the west of the hedgerow, approximately 30 m into the field, one column was between the hedgerow and the sown field margin plots, and a further six columns of traps were in the field to the east of the field boundary. The total area enclosed by the four corners of the grid of traps was 6996 m^2. The total effective area trapped was calculated by adding an external border to the area equivalent to half the distance between traps in each dimension. This increased the area to 8268 m^2. At each of the 156 grid intersections, three pitfall traps were set in a triangular arrangement, approximately 0.5 m apart, giving a total of 468 traps. The pitfall traps were operated dry with a little soil and a few stones in the bottom to provide shelter and were protected from the rain and predation by birds by inverted plastic plant pot saucers supported above the traps on wire legs.

Trapping commenced on 5 June 1994 by removal of the trap lids. Beetles captured overnight were identified, sexed and marked in the field on the following day. Beetles were held by elastic bands on a length of wooden dowel and permanently marked by abrading small areas of the elytra and pronotum with a model-maker's drill fitted with a slitting disc, as described by Thomas (1995). A system of ten possible marking positions on the elytra and pronotum, denoting the numbers (1, 2, 4, 3, ... , 512), allowed a maximum of 1023 beetles of each sex to be individually marked.

The lids were replaced on the traps and the beetles released at the site of capture, so eliminating potential bias from individuals falling in traps for a second time immediately after release and avoiding disruption to any possible "territorial" behavior. The trap lids were removed again on the following day. Beetles were thus able to mix and disperse freely over the experimental site for at least 24 h before being exposed to the possibility of recapture. The position and identity of recaptured beetles and the number of newly captured beetles were recorded and the previously unmarked beetles were given marks. Trapping continued on alternate days until 17 August 1994 when the experiment was terminated to allow the crop to be harvested. Frequent sampling enabled the traps to be well maintained throughout the experiment, keeping the rims flush with the soil surface and adding soil to fill cracks around traps as necessary. Escapes (potentially 4% a day; Luff 1975) were minimised by periodically cleaning the inner surface of the traps.

Regression models were fitted to frequency distributions using a non-linear regression procedure in GENSTAT 5 (Lawes Agricultural Trust). SADIE analysis was performed with 200 simulations per test, on pairs of data sets to derive two indices of association, I_t and I_m, to test for the spatial stability of the pattern of aggregation over time. Meteorological data were obtained from a weather station situated in a neighbouring arable field, approximately 1 km away.

Results

Activity-density

Mean daily temperature, total daily rainfall and the total daily catch of male and female *P. melanarius* are given in Fig. 1, showing the changes in activity-density over the experimental period. Four main periods of activity-

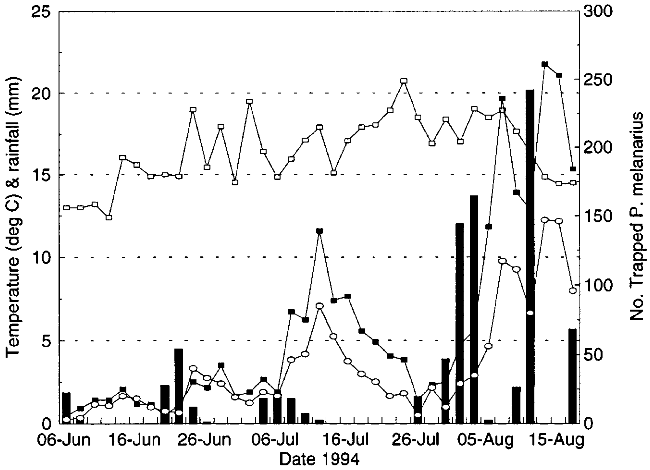


Fig. 1 Total captures of male (*filled squares*) and female (*open circles*) *Pterostichus melanarius* in 468 pitfall traps on alternate days between 6 June and 17 August 1994 with mean daily temperature (*open squares*) and total rainfall over 2 days (*black columns*)

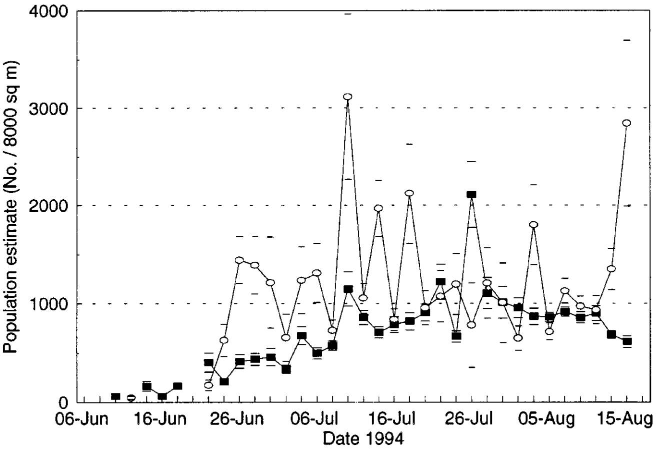


Fig. 2 Population density (area approximated to 8000 m^2) of male (*filled squares*) and female (*open circles*) *P. melanarius* estimated by the Jolly-Seber method, for each day with sufficient recaptures between 6 June and 15 August 1994. The standard error of mean is indicated by *horizontal lines* above and below the mean value

density are clear from the successive peaks. These peaks were unrelated to the mean daily temperature but each of the four periods of rising and falling activity-density appeared to be related to relatively discrete periods of rainfall: 1–7 June (15.2 mm), 19–25 June (7.9 mm), 3–12 July (5.6 mm) and 25 July–4 August (31.4 mm) with a further 28.1 mm on 9, 10 and 16 August. Because activity-densities declined during dry periods then increased after rain, we speculate that dry periods caused a decline in activity, and that subsequent rainfall might then have triggered periods of renewed activity. If a constant or steadily increasing population density is assumed, then four periods of activity can be inferred from the data in Fig. 1: 6–20 June, 21 June –2 July, 4–26 July and 28 July–15 August.

Density

Individually marked beetles allowed use of the Jolly-Seber method (Jolly 1963, 1965; Seber 1973) to estimate population densities (±standard errors) (Fig. 2). The estimate of the male population density increased up to the second week of July, after which the population size remained fairly stable. The female population estimates showed a similar pattern but fluctuated more widely and standard errors were larger. For the period between 12 July and 13 August, when the maximum population size appeared to have stabilised, the average of 17 population size estimates ±95% confidence limits (c.l.) was 957 ± 169 males and 1163 ± 219 females, giving a combined estimate of 0.26 beetles m^{-2}. Using only data of the more abundantly captured males, absolute density estimates were also calculated for each field, excluding data from the central column of traps between the hedgerow and the sown plots. Mean population sizes over the period 12 July to 13 August ±95% c.l. in the fields to the west and east of the hedgerow were 531 ± 85 and 458 ± 193, respectively. Total captures over the same period were 1145 and 568, respectively, suggesting higher activity in the west than in the east field.

Activity

Number of recaptures

A total of 1009 males and 768 females were successfully marked between 6 June and 15 August. A small number of beetles injured during marking or wrongly marked were killed at the time of marking to avoid subsequent bias or confusion. 1198 male and 485 female recaptures were made, including multiple recaptures. A sub-sample of 750 male recaptures was used for the analysis of activity, since this adequately described the frequency distributions of dispersal distances. The relative frequency (Rf) of recaptures is shown in Fig. 3. Non-linear regression showed an exponential decline in the Rf of number of times beetles were recaptured (Nr) for males ($P < 0.001$, variance accounted for = 99.0%; $\mathrm{Rf} = -0.009 + 0.437 \times 0.604^{\mathrm{Nr}}$) and females ($P < 0.001$; variance accounted for = 99.9%; $\mathrm{Rf} = -0.003 + 0.597 \times 0.423^{\mathrm{Nr}}$). Of the marked male beetles, approximately 40% were never recaptured and approximately 60% were recaptured at least once. Approximately 60% of females were never recaptured. The maximum number of times a beetle was recaptured was ten for a single individual male and five for five females.

Although the Jolly-Seber method used above does not assume a closed population, an indication of the openness of the experimental arena was obtained by calculating the recapture rate of marked individuals released in different columns of the grid. The north and

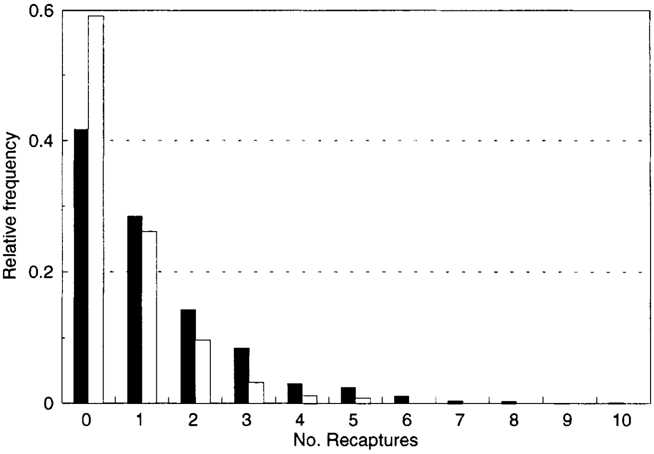


Fig. 3 Relative frequency distribution of number of recaptures of individually marked *P. melanarius*. Sample size 1009 males (*filled columns*) and 768 females (*open columns*)

south ends of the arena were enclosed by a track and a hedgerow, while the east and west borders of the grid of traps were in the open field, permitting movement to and from the rest of the field. The recapture rate of marked beetles released in each column of traps was approximately 60% across the whole arena except in the columns within the field at the edges of the grid where only 50% of beetles were recaptured.

Time and distance between recaptures

The majority of recaptures were made within 3 weeks of release and within 35 m of the release site. Similar patterns are shown by both sexes (Fig. 4). A slightly greater proportion of females than males was recaptured more than 30 days after release, but there was no clear difference in the distances between recaptures of male and female beetles. In both sexes, a small number of individuals were recaptured at large distances after short times, but more were recaptured only a short distance from their sites of release after long time intervals.

Daily displacement distances

The frequency distribution of 1-m daily displacement distance classes declined exponentially with increasing distance for both male and female beetles (Fig. 5). Nonlinear regressions using an exponential model were significant ($P < 0.001$) for both sexes with 94.4% and 94.8% of the variance accounted for in the distribution of males and females, respectively. The relative frequency of males (F_m) and females (F_f) against distance (d) (SE in parentheses) was: $F_m = 0.28\ (0.35) + 28.63\ (1.42) \times 0.69^d\ (0.02)$ and $F_f = 0.29\ (0.36) + 33.67\ (1.59) \times 0.63^d\ (0.03)$, respectively. General linear modelling showed no significant differences between the slopes, but a significantly greater intercept ($F_{1,\ 58}$, $P < 0.05$) for females than males.

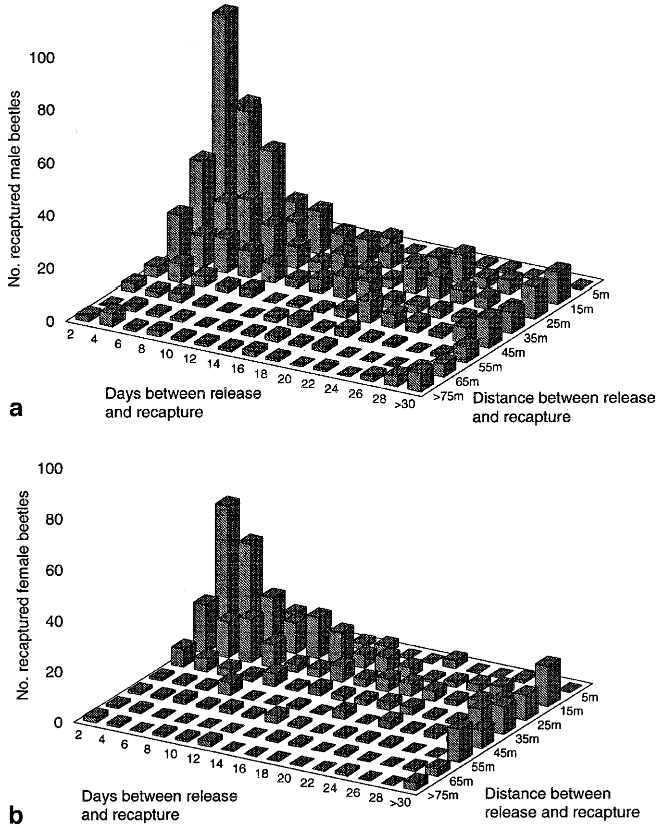


Fig. 4 Number of recaptures of male (**a**) and female (**b**) *P. melanarius* plotted against the distance and time between recaptures

Changes in activity over time were also estimated by calculating the daily dispersal distances for cohorts of beetles released on each day throughout the experiment (Fig. 6). Cohorts containing less than three individuals have been omitted. Both sexes exhibited larger means or ranges of dispersal distances which correspond to the pattern of activity-density shown in Fig. 1, and higher mean dispersal distances in August. Overall the males released in June and July were more active than the females, and females released during August were more active than males, but these differences were not significant. Table 1 summarises the data on daily dispersal distances by activity period in more detail. Coefficients of variation for each period of activity-density indicated a marked decrease in variation of dispersal distances during August.

Diffusion

The distributions of times and distances between recaptures for male and female beetles allowed diffusion coefficients to be calculated. Although the recaptures were made at different times and locations within the experimental arena, the individual movements are assumed to be equivalent to what would have been observed if the beetles had been released from a point-source. Treating the males ($n = 750$ recaptures) and females ($n = 485$

recaptures) separately, the data were fitted to the following model, using maximum likelihood, to derive a diffusion coefficient (D) where $D = (1/4n)\sum \frac{r_i^2}{t_i}$, where r is the distance between release and recapture site and t is time between recaptures. Diffusion coefficients (standard errors in parentheses) for male and female beetles were 27.90 (0.59) m^2 day^{-1} and 23.65 (0.62) m^2 day^{-1}, respectively. A test statistic for differences between diffusion coefficients was defined as $X_i^2 = 2 \times \ln\left\{\frac{\hat{D}^{n_1+n_2}}{\hat{D}_1^{n_1}\hat{D}_2^{n_2}}\right\}$ where D_1 and D_2 are the coefficients for males and females respectively, D is the weighted mean and n is the number of observations (P. Brain, personal communication). The value for X^2 was calculated as 7.85 ($df = 1$), indicating the two diffusion coefficients to be significantly different ($P < 0.05$). The data for both distributions were, however, under-dispersed, indicating that more individuals moved shorter distances than expected for a diffusion process.

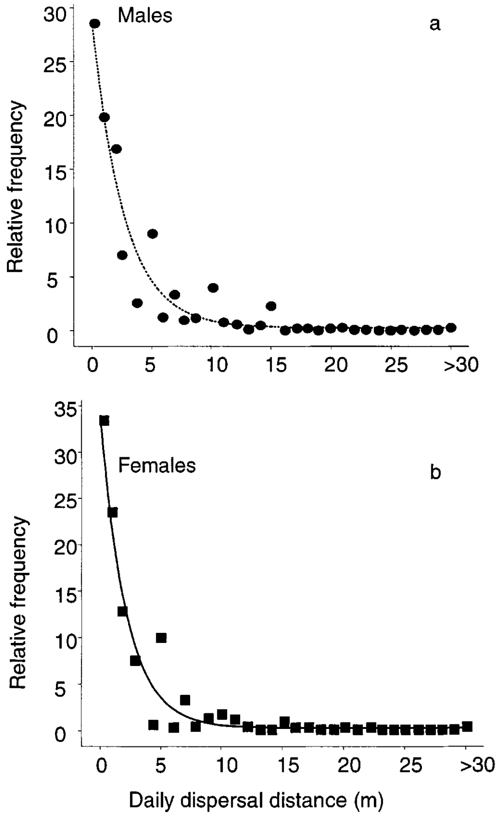


Fig. 5 Relative frequency distribution of minimum daily displacement distances in 1-m distance classes of *P. melanarius* males (**a**) and females (**b**)

Distribution stability

The pitfall trap data were plotted as contour plots (Fig. 7) to show the two-dimensional distribution of activity-density over the whole grid. The extensive data set permitted 37 contour plots to be drawn; however, for concise presentation, we show only the accumulated activity-density during each of the four main periods of activity apparent in Fig. 1. Visual inspection of Fig. 7 clearly indicates an aggregated distribution of activity-density over the arena, with higher numbers of beetles trapped on the west than on the east side of the field boundary, and a number of "hot-spots" of relatively high activity-density. The general pattern persisted

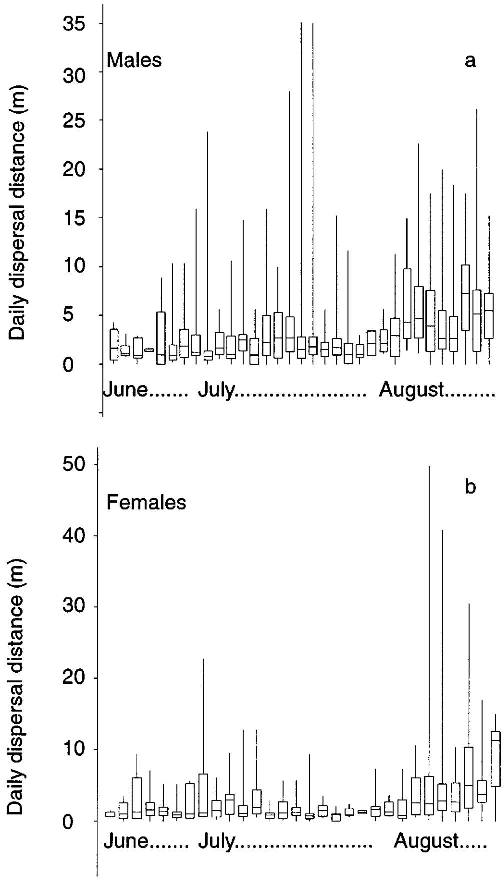


Fig. 6 a,b Box and whisker plots of minimum daily dispersal distances for cohorts of *P. melanarius* released on different days between June and August 1994. Cohorts with less than three individual recaptures are omitted. **a** Males: alternate days from 10 June to 15 August **b** Female: 12 June, and alternate days from 20 June to 15 August

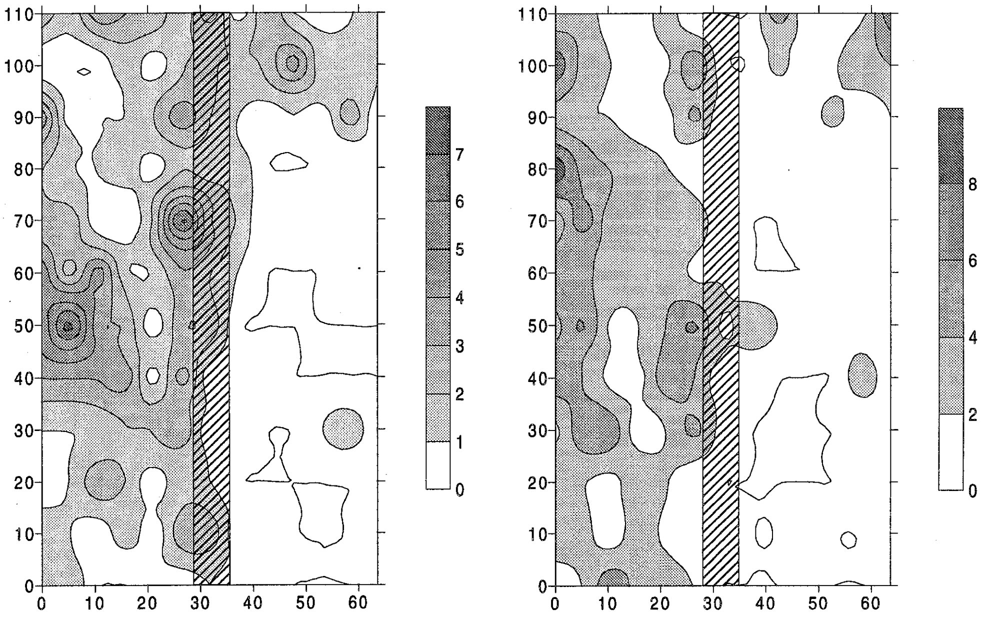
Table 1 Mean daily dispersal distances (m day^{-1}) (±95% confidence limit in parentheses) for each activity period. *Different letters* denote significant differences ($P < 0.01$) by non-parametric Kolmogorov-Smirnov test (*CV* coefficient of variation)

	6–20 June	21 June–2 July	4–26 July	28 July–15 August
Mean	2.62 (2.11)a	2.42 (0.7)ab	2.76 (0.4)ac	5.18 (0.6)d
CV	167%	149%	144%	92%

throughout the summer and appeared to be quite stable. SADIE analyses of spatial association between each distribution were carried out using 200 simulations for each test. Indices of association and their probabilities are given in Table 2. The spatial distribution of counts between each successive period (1 vs 2, 2 vs 3 and 3 vs 4) and between periods 2 and 4 were all positively and significantly associated, according to both indices of association ($I_t > 1$, $I_m > 0$; $P_t < 0.025$, $P_m < 0.025$). The spatial association of the distributions of activity-density between periods 1 and 3 and between periods 1 and 4 were also positive but not significant.

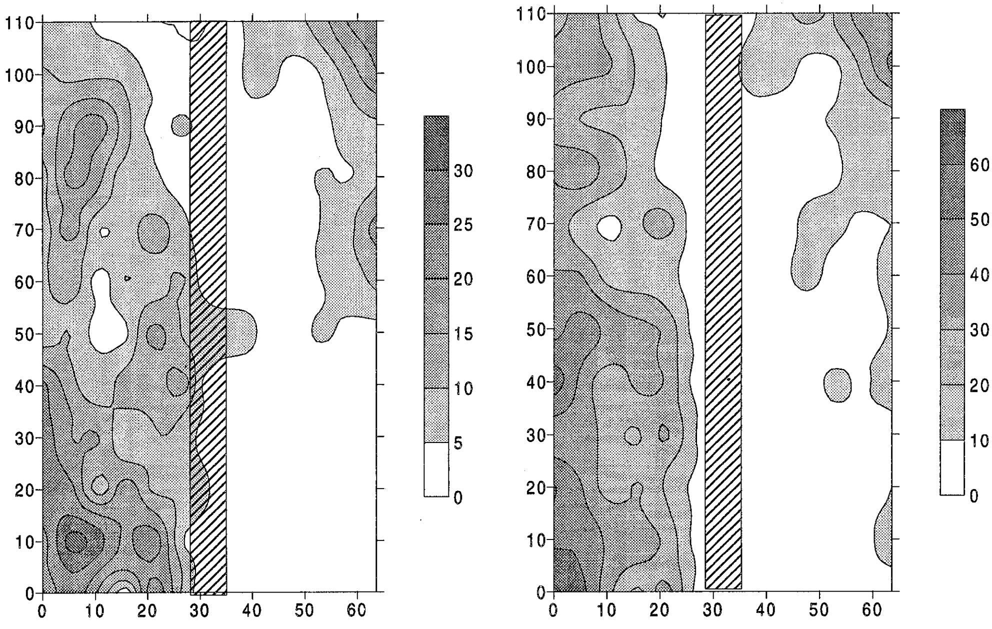
Movement between fields

The effect of the field boundary on limiting movement of beetles between fields was estimated by comparing the numbers of beetles released and subsequently recaptured in different halves of the grid of traps (Table 3). Movement between the northern and southern sections of the field site required no crossing of a field boundary, while movement between the east and west fields necessitated traversal of the 5.3-m hedgerow. Of the 750 male and 485 female recaptures, 24% of males and 26% of females released in the northern half were recaptured in the southern half of the field; 16% of males and 16% of



Activity-density 6 June - 20 June

Activity-density 21 June - 2 July



Activity-density 4 July - 26 July

Activity-density 28 July - 15 August

Fig. 7 Spatial distribution of accumulated activity-density over the experimental site for the four periods of activity-density apparent in Fig. 1. Levels are number of *P. melanarius* captured per trap site. Contours were fitted by kriging. In each contour plot, the hedgerow is represented by the *vertical hatched bar*. Axes are in metres from the pitfall trap site at the south-west corner of the grid females released in the southern half were recaptured in the northern half of the field. Movements through the hedgerow between the two fields, although requiring a smaller scale of movement, were lower: 7% of males and 11% of females released on the east side of the hedgerow were recaptured on the west side and only 3% of males and 2% of females released on the west side of the hedgerow were recaptured on the eastern side.

Discussion

Marking for release and recapture studies often involves collecting beetles from the field, transporting to and marking in the laboratory and releasing them later, not necessarily at their original site of capture. These methods are thought to stress the animals in such a way that, following release, their activity can be increased during the so called "disturbance dispersal period" (Greenslade 1964b). We attempted to minimise errors arising from the influence of handling on beetle activity by using the method of Thomas (1995). The beetles also appeared to be unaffected by the marking method. A number of individuals marked as early as July were recaptured in October and November during further studies on *Nebria brevicollis*. Furthermore, a single *Abax parallelepipedus* marked in July the previous year (1993) was recaptured 12 times during the summer of 1994.

Rising and falling activity-density of *P. melanarius* revealed by the frequent sampling used in this study is probably typical of other pitfall trap studies of this species (e.g. Greenslade 1965; Desender et al. 1985). In many studies, however, sampling is normally less frequent and often intermittent, for example, 1 week in 4 (Kendall et al. 1995). At such levels of resolution, rather than observing a smooth time series, activity-density can appear more erratic. The onset of peaks of activity-density shown in Fig. 1 appear to be correlated with periods of rainfall, which in this study occurred during fairly discrete periods. It is likely that the timing and amount of rainfall can affect activity-density through a number of processes. There may be a reduction of activity during dry periods, or prey items, for example slugs, may become unavailable. Indirect effects on observed activity may arise from the fact that many soil types contract during dry periods, creating deep fissures in the upper layers. This phenomenon was observed on the heavy clay soils of our study site and may have increased the effective surface area of the field, thus reducing the effective trap density. Similarly, deep cracks in the soil may act as temporary pitfalls, reducing the probability of encountering traps. After rain, these effects can be reversed at a rate dependent on the soil type, drainage and amount of rainfall. Further controlled studies would be required to quantify the magnitude of direct and indirect effects of rainfall on behavior. Clearly, the unpredictable nature of the weather means that intermittent sampling regimes are likely to trap randomly during troughs or peaks in activity-density, possibly giving data which are difficult to interpret, if not spurious, especially if they are compounded with treatment effects.

Table 2 Output of SADIE analysis for association between the spatial distributions of two sets of counts. Data sets associated if $I_t > 1$ or $I_m > 0$. Data sets are dissociated if $I_t < 1$ or $I_m < 0$. Significant associations indicated if $P < 0.025$. Periods *1–4* are the activity-densities (pitfall trap counts) associated with the periods 6–21 June, 22 June–3 July, 4–25 July and 26 July–17 August in Fig. 1. Each analysis used 200 simulations

Period		1	2	3
2	I_t	1.188	–	–
	P_t	0.0025	–	–
	I_m	3.239	–	–
	P_m	0.005	–	–
3	I_t	1.190	1.299	–
	P_t	0.14	0.0025	–
	I_m	0.921	5.230	–
	P_m	0.273	0.0025	–
4	I_t	1.263	1.373	1.375
	P_t	0.07	0.0025	0.0025
	I_m	2.515	5.456	9.068
	P_m	0.028	0.0025	0.0025

Table 3 Recaptures of individually marked male (*m*) and female (*f*) *P. melanarius*, released in one-half of a grid of traps. Movements east (*E*) ↔ west (*W*) are between fields requiring movement through a hedgerow; movements north (*N*) ↔ south (*S*) are within fields

Released in		Recaptured in	m	f
W	→	W	536	388
W	→	E	18	8
E	→	W	13	10
E	→	E	183	79
S	→	S	305	244
S	→	N	58	45
N	→	S	91	51
N	→	N	296	145

In contrast to the four peaks of activity-density, the estimates of absolute density, especially for male beetles, showed a steady increase in numbers between June and early July, after which the population size remained relatively constant. The Jolly-Seber method, in common with other mark-recapture techniques, is sensitive to low capture rates. This occurred on a number of occasions and population density is likely to have been over- or under-estimated, depending on the number of recaptures in the small samples. Low capture rates during the first 2 weeks and on occasional days between activity-density peaks have led to no density estimates being made on some days and some estimates having large standard errors.

Few absolute density estimates of *P. melanarius* have been made in cereal fields. Our estimate of 0.26 m^{-2} is low, but falls within the range of other estimates using a variety of techniques. Desender et al. (1985), quoting other sources, compared estimates of 0.03–8 m^{-2} in arable fields, with their own estimate of 15–22 m^{-2} in grassland using barriered pitfall traps. Purvis and Fadl

(1996) using emergence traps found densities of 13.8 and 2.5 m^{-2} in winter and spring cereals, respectively. Other mark-recapture studies provide more comparable estimates of 0.73 m^{-2} (Ericson 1977) and 0.69 m^{-2} (Thomas et al. 1997). The latter estimate was made on a part of the same field site used in the present study during a pilot study in the previous year. Absolute population estimates for woodland habitats, quoted from other sources by Desender et al. (1985), range from 0.06 to 2.5 m^{-2}. Generally, it appears that population densities of *P. melanarius* increase as habitat changes from woodland to arable fields to grazed pasture. The true field density in the present study is likely to be slightly higher than the results suggest, since our study site also incorporated a wide hedgerow habitat with low activity-density. Clearly, population density estimates will vary according to the scale of sampling and the scale of population aggregation. Grids of traps should be large enough to sample at a scale above the size of the population's constituent patches. Recent work at the scale of multiple fields (N.J. Brown and C.F.G. Thomas unpublished) suggests that the size of the grid used in the present study, although large, may still be inadequate to extrapolate population density estimates of whole fields.

Overall, the activity of males was higher than that of females, especially during June and July, but females became more active during August (Fig. 6). However, our data do not show the range of male and female displacement distances to be very different (Fig. 4), although a slightly, but significantly, higher relative proportion of females occurred in the smallest displacement distance class (Fig. 5). The diffusion coefficient for females was also significantly lower than that for males and the observation of lower female activity-density, and higher absolute density, also implies lower female activity. Moreover, more females than males were never recaptured, and the mean number of multiple recaptures per individual was lower for female than male beetles, suggesting lower female activity or subtle behavioral differences that lower the probability of females falling into pitfall traps. However, sprint speeds and move lengths between turns of *P. melanarius* have been shown to be greater for females than males (Wallin and Ekbom 1994), suggesting higher female activity, although Fig. 1 in their paper shows similar movement for hungry males and females but reduced speed of movement for satiated females.

The activity of *P. melanarius* in the present study resulted in mean minimum daily displacements of approximately 2.5–5 m. Studies using radar tracking have shown mean speeds of 2.4 m h^{-1} resulting in net displacements of 5.3 m day^{-1} (Wallin and Ekbom 1988). Sprint speeds of 3 m min^{-1} and net displacements of approximately 4 and 9 m h^{-1} have also been demonstrated (Wallin and Ekbom 1994). The range of displacement distances was large in this (maximum 112 m after 4 days, minimum 0 m after 28 days) and other studies using mark-recapture methods, e.g. 0.4–44 m day^{-1} (Wallin and Ekbom 1988), 4–58 m day^{-1} (Lys and Nentwig 1991), 4–73 m day^{-1} (Lys and Nentwig 1992). No other estimates of diffusion rates for *P. melanarius* could be found in the literature. However, a diffusion coefficient of 35 m^2 $week^{-1}$ determined for *A. parallelepipedus*, a similar-sized beetle of wooded habitats (Petit and Burel 1993) is somewhat lower than our estimate of approximately 24–28 m^2 day^{-1} for *P. melanarius*.

These estimates of activity suggest that *P. melanarius* has a potentially high dispersal power. In spite of this, the spatial pattern of activity-density stayed the same for considerable periods and few individuals were captured at distances greater than 55 m from their release sites after 30 days. Several individuals were recaptured close to their release position up to 4 months later. Although approximately 50% of marked beetles were never recaptured, the greatest proportion of the recaptures appeared to show a tendency to remain within a limited area. The stability of the activity-density distribution patterns need further study to be fully explained. Possible causes might include aggregation in stable areas of high prey density, preferred microclimatic conditions or edaphic factors creating preferred sites for oviposition and larval survival, resulting in aggregated adult emergence. The fit of the diffusion model was poor because of under-dispersed data, indicating that more individuals moved shorter distances than would be expected in a diffusion process. This provides further evidence of dispersal behaviour deviating from a random walk. Although other studies have suggested that a correlated random walk best describes the movement behavior of *P. melanarius* (Wallin and Ekbom 1988), resulting in displacement distances greater than predicted from a random walk, our data suggest that displacement distances are smaller, and that there is some affinity to particular locations.

Compared with the rate of movement of marked individuals between areas within fields, movement between fields was greatly reduced by the presence of the hedgerow. Our relative estimates comparing the movement between and within fields are conservative, since the dimensions of the grid for movement within fields was twice that for movement between fields. Other studies involving invasive methods have also demonstrated the role of field boundaries as barriers to movement (Mauremootoo et al. 1995). Modelling carabids as metapopulations in farmland has shown the rate of dispersal across field boundaries to be a critical factor for population survival in some intensive agricultural systems (Sherratt and Jepson 1993). However, despite much interest in metapopulation dynamics, there are few models of species in agricultural systems, because of a lack of field data on population dynamics and dispersal (Halley et al. 1996). The aspects of activity presented here have provided some empirical data for *P. melanarius* and have general implications for representing carabid dispersal in metapopulation models. Diffusion coefficients determined from within-field studies cannot be directly extrapolated to model movement at larger scales, because interactions between populations in adjacent fields are significantly reduced by field boundaries. Other landscape features, for example roads and rivers, may be permeable to beetles to greater or lesser degrees than the hedgerow in the present study (Mader et al. 1990) and differ between species. For a given population density, aggregated in patches within fields, expected encounter rates with and movement across boundaries may also be below those predicted by simple diffusion models.

Acknowledgements This work was funded under the EC AIR3 programme, Grant no. AIR3-CT 920476 and formed part of a larger study, "Field boundary habitats for wildlife, crop and environmental protection". IACR-Long Ashton receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom. Many thanks to P. Brain for statistical advice, and to M. Hamacher and N. Cahill for essential weekend assistance in the field.

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