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Within field movement of overwintered Colorado potato beetle: a patch-based approach

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Abstract: After comparing the persistence of four marking techniques, a mark–release–resight study was performed to characterize mid-season movement of the Colorado potato beetle [*Leptinotarsa decemlineata* (Say); Col., Chrysomelidae] simultaneously in a fallow and in a wheat field. Isolated patches of potatoes were installed in a random spatial arrangement on both fields similarly. Overwintered beetles were individually marked and released. Beetles showed limited inter-patch movement activity (15.9% of recovery events) with an overall mean daily dispersal of 0.309 m (0.0–7 m). There was a significant difference in the insects' movement distance between the fallow and wheat field but there was no difference between the movement distances of males and females. The distance between the patches varied between 1 and 7.81 m, and inter-patch movement was infrequent (15.9%). Results suggest that surrounding fields by wheat rather than fallow grounds should be studied as a possible strategy to reduce the movement of overwintered beetles between potato fields.

Key words: *insect marking*, mark–release–resight, inter-patch movement

1 Introduction

The Colorado potato beetle (CBP), *Leptinotarsa decemlineata* (Say), is the most destructive insect defoliator of potato, *Solanum tuberosum* L., in North America and Europe (Jermy and Sáringer 1955). The economic impact of this pest has been increasing because of its rapid development of resistance to all major classes of modern synthetic insecticides (Forgash 1985). The important yield losses that can occur in spite of insecticide use continues to encourage researchers to turn their attention to ecologically oriented management approaches (Hare 1990; French et al. 1993). A better knowledge of the recruitment of CPB in potato fields and on the movement pattern of CPB adults is of significant importance in pest management decisions.

The geographic distribution of the CPB suggests that the adult CPB is an able disperser. It spread across the United States and Europe at rates of 100–150 and 50–60 km/year, respectively (Follett et al. 1996). Small-scale observations on the dispersal of adult CPB suggest a season-dependent activity (Weber and Ferro 1994b); in the early season, beetles move from overwintering sites to potato fields (post-diapause movement), in the mid-season beetles move mostly within the potato fields while in the late season, they move from the potato fields to overwintering sites (prediapause movement). Spring adults often cover distances up to several hundred metres over a few days on bare soil (review in Boiteau et al. 2003), and only a small proportion of adult beetles disperse more than 500 m from their overwintering sites (Follett et al. 1996; Boiteau et al. 2003). Successful host location by overwintered CPBs was negatively correlated with the distance between the previous and present year location of potato fields (Weisz et al. 1994; Hough-Goldstein and Whalen 1996). Moreover, the physical characteristic of the border crop significantly influenced the recruitment of potato fields (Weisz et al. 1994). These and other studies on CPB dispersal, however, focused chiefly on the inward (early season) or outward (late season) dispersal or host location of the CPB using mark–release–recapture technique (Boiteau 1986, 2001; Caprio and Grafius 1993, Jermy et al. 1988; Follett et al. 1996; Noronha and Cloutier 1999), whereas the number of studies on within-field or mid-season movement are rather limited. Indirect observations examining insecticide resistance (Heim et al. 1990; Tisler and Zehnder 1990) or spatial structure (Blom and Fleischer 2001; Blom et al. 2002; Boiteau 2005) of CPB populations suggest only restricted movement activity in the mid-season.

A better knowledge of CPB movement within field is critical to the assessment and application of cultural management tactics such as trap cropping (Hoy et al. 2000). The primary aim of the present study was to quantify the mid-season movement rate of the CPB using the mark–recapture technique. The first objective was to select the most persistent marking technique by carrying out a laboratory comparison of four marking techniques. The second objective was to determine the dispersal rate – whether it differs between male and female and whether it is influenced by the density of non-host vegetation. This objective was achieved by assessing the movement of individually marked CPB adult beetles among patches of potatoes in a fallow and within a wheat field.

2 Materials and Methods

2.1 Selection of marking technique

Several marking techniques have been developed for individual marking of CPB adults. Elytral punctures (Unruh and Chauvin 1993), bee markers (Szentesi 1985; Weber and Ferro 1994b), enamel paints (Jermy et al. 1988) and paper labels (Caprio et al. 1990) are the most frequently used methods. Although elytral punctures are permanent, their recoding might be time-consuming. Thus, two types of tags (bee marker and paper label) and two types of adhesives (shellac and an instant bond) were tested (a total of four combinations, referred later as marking techniques). Bee marker and shellac were the parts of a Queen Marking Kit (Bienen-Voigt and Warnholz Gmbh and Co.Kg, Ellerau, Germany), paper labels (size: 3×4 mm) were produced using copy paper, while Loctite (Loctite Ireland Ltd., Dublin, Ireland) was used as instant bond. A total of 40 beetles collected from potato fields at the Ecological Station of the Plant Protection Institute of the Hungarian Academy of Sciences, were marked by gluing one of the marking tags on the left elytra of each beetle. According to our previous experience, glued beetles behaved naturally and were capable of flying (Á. Szentesi, pers. obs.). Each group of 10 beetles with the same treatment was placed in a separate greenhouse cage and provided with a potato plant. Each beetle was sexed and classed as old, overwintered or newly emergent summer adult. Beetles were checked twice a week until all beetles within a group had lost the marking tag. Survival time analysis was used, rather than the traditional chi-squared test, because it can consider the time at which each tag is lost as a dependent variable. The chi-squared test of the 'Survival Analysis' module (not equivalent with the traditional χ^2 test) of the STATISTICA computer program (StatSoft Inc. 2003) was performed to test for general differences in the persistence of several marking techniques. Gehan's Wilcoxon test by the STATISTICA computer program (StatSoft Inc. 2003) was applied to compare the persistence of the two marking techniques.

2.2 Field experimental design

The field experiment was carried out at the Ecological Station of the Plant Protection Institute. The station is located in the Buda Hills (47°32′53″N, 18°55′59″E), at about 310 m above sea level. Two experimental areas (7×7 m each) were selected out of a wheat field and a fallow field planted with alfalfa in the previous year. Both experimental areas (hereafter called as fields: wheat and fallow) were at least 100 m from any previous- and present-year potato field or any overwintering site. This distance should have protected the experimental areas from any significant colonization by newly emerging overwintered CPBs (Boiteau et al. 2003). Within each area, 49 (7×7) positions were marked in an evenly spaced arrangement. Twelve of 49 positions were randomly selected, and the same 12 positions were used for both fields. In each selected position, a patch of potatoes was installed 20 days before the start of the experiment. The experimental patches of potatoes were made up of potted plants (pots of inner diameter 38 cm). Each pot was sunk below ground level and contained three potato plants (cv. Vital) at a distance of approximately 20 cm from each other.

During this procedure, special attention was paid to avoid physical disturbance of the wheat. The distance between the patches (range 1–7.81 m) was matched with the daily movement distance of the CPB as suggested by Weber and Ferro (1994a). Three days before the start of the experiment, about 200 beetles were collected in a potato field. All of them were overwintered adults. Each beetle was sexed and marked using bee tags and shellac. Until the start of the experiment, beetles were kept in cages (capacity: approximately 20 l) under a natural light and temperature regime with access to a potato plant.

Three male and three female individually marked CPBs were released on each patch at the start of the experiment on 5 June 2004, which is the mid-season time for the CPB in Hungary. The experiment started more than 1 month after finding the first overwintered beetles in a nearby potato field, and ended before plant phenology or photoperiod (Weber and Ferro 1994b) would initiate diapause. Although a recent study revealed that the within-field movement of the adult CPBs in the mid-season were not density-dependent (Sandeson et al. 2004), it is important to note that the number of released beetles did not exceed the density of beetles previously observed in the potato fields in Hungary at this season (Jermy et al. 1988). The position of each beetle was recorded daily by carefully examining the patches of potatoes until the recovery rate decreased below 50%. Release and scouting of the beetles were carried out between 05.00 and 09.00 hours when beetles show limited dispersal activity (D. Schmera, pers. obs.).

At the start of the experiment, the potatoes in the patches were 50 cm high while the wheat was 85 cm tall. Although the small patches of potatoes, which remained isolated during the whole study, did not simulate the spatial distribution of host plants in commercial potato fields in the United States and Europe, they might be similar to the spatial distribution of the original host plants of the CPB in the arid and semiarid areas of Mexico and the United States (Jermy and Sáringer 1955).

2.3 Measuring beetle movement

The beetles' daily movement was characterized by analysing movement events. By definition, each recovery together with any previous sighting was regarded as a movement event, as the sight and the recovery coordinates of the potato patches together defined the direction and the distance of the movement, whereas the time elapsed between the two events determined its duration. Only 1-day movement events were analysed.

Each movement event was first coded as 'stay', if the beetle stayed in the patch and 'move', if the beetle moved into another patch (i.e. the movement distance was equal or more than 1 m). The other factors considered in the analysis were: field (fallow or wheat), sex (male or female), and recovery date (in days from the start of the experiment). A log-linear analysis of frequency tables of movement events was then performed to test the effect of individual factors and the possible relationships among them. Log-linear analysis is a basic and straightforward method for analysing multi-way frequency tables (StatSoft Inc. 2003). In the present study, the effects 'field' and 'sex' were *a priori* two-categorical factors, whereas movement was not. Movement distance was transformed into 'stay' or 'move' categories because: (1) these categories can be well interpreted biologically, if our interest focused on whether the beetles stayed or not on the patch and (2) inter-patch movement of the beetles was infrequent. The log-linear analysis was performed by the STATISTICA computer program (StatSoft Inc. 2003). An automatic selection algorithm of the log-linear analysis was applied to find a best-fitting model to the data (P = 0.1 was used to judge whether a model fits the data and P = 0.05 was used to judge whether an effect or set of effects in a model contributed significantly to the fit of the model). The ratio of the number of beetles recovered in the same patch over the total number of recovered beetles between the two fields was compared by the difference test module of the STATISTICA computer program (StatSoft Inc. 2003).

The non-parametric Kruskal–Wallis test and Mann–Whitney U-test were applied to compare movement distances of the CPB. If Kruskal–Wallis test proved to be significant, non-parametric Tukey's test (Zar 1999) was applied to detect differences. The application of a non-parametric test was necessary as the distribution of the movement distances was skewed. We used P = 0.05 as the significance level.

3 Results

3.1 Selection of marking technique

The persistence of the four marking techniques was significantly different ($\chi^2 = 16.575$, d.f. = 3, P < 0.001; fig. 1). Bee markers with shellac were the most persistent (fig. 1) with 70% of the beetles retaining their tags 18 days after the marking. The application of bee tags was significantly more persist-

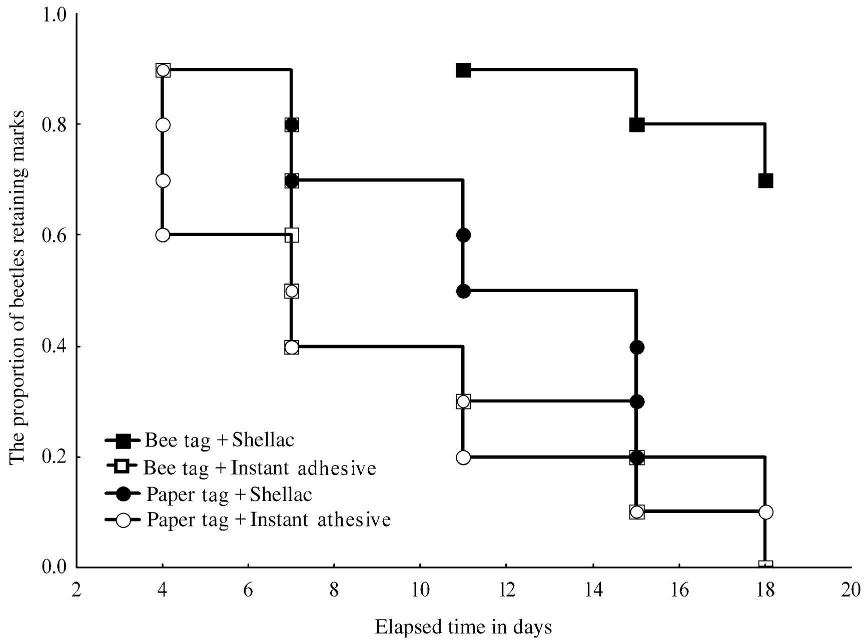

Fig. 1. *The comparison of the retention of marking tags*

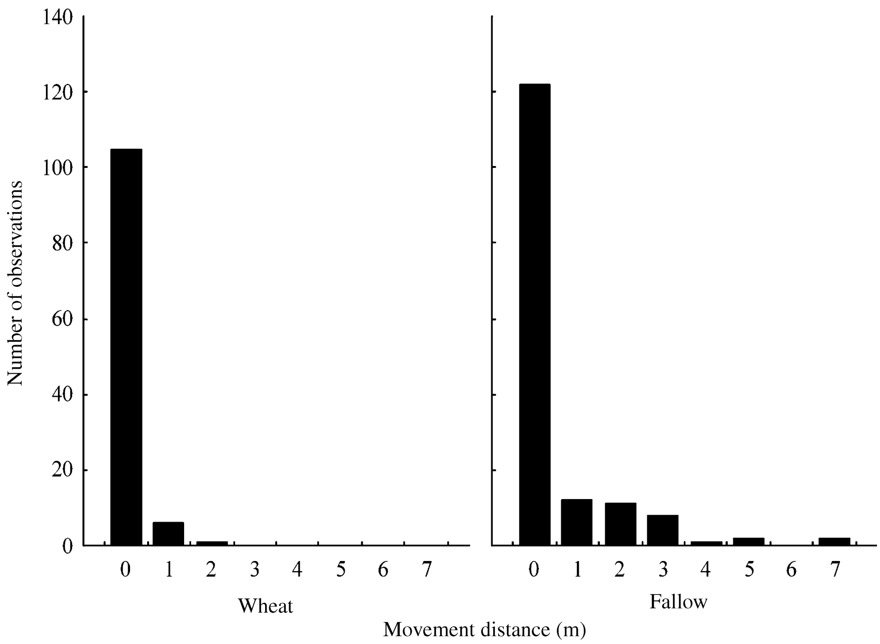

Fig. 2. *The frequency distribution of the movement distances (altogether 270 1-day movement events were recorded)*

ent (Gehan's Wilcoxon test: G = 2.771, P = 0.006) than the application of paper label together with shellac. In contrast, each beetle lost its bee tag glued by instant adhesive after 18 days. The parallel application of bee tag and bee glue was not affected by beetle age (Gehan's Wilcoxon test: G = 1.246, P = 0.213) or sex (Gehan's Wilcoxon test: G = 0.984, P = 0.325).

3.2 Recovery rate and frequency distribution of recovery events

During the experiment most days were sunny; the temperature varied between 12.4 and 29.5°C, and the beetles' behaviour was natural. The ratio of marked to released beetles was 59.7%, 54.8%, 57.6% and 48.6% on the first, second, third and fourth experimental days, respectively. On the fourth day, the ratio of recovered beetles dropped below 50%, thus the experiment was terminated. Altogether, 270 one-day recovery events were recorded. The frequency of these movement events was significantly different between the experimental dates (table 1). We observed 101 recovery events on the first experimental day, and 65, 51 and 53 events in the second, third and fourth days, respectively. The frequency of recovery events was significantly different in the two fields (table 1): more 1-day recovery events were recorded in the fallow field (158) than in the wheat field (112). Of the 270 1-day recovery events, 43 inter-patch (movement distance was more than 0) movements were recorded while most beetles (227) remained within the patch (i.e. stayed). This ratio is significantly different from the theoretical 50% (table 1). The recovery event frequency of male (133) and female (137) beetles was not significantly different (table 1). Of the six two-way interactions, the factor pair of field and movement, and the factor pair of recovery date and movement were the most important for explaining the recovery pattern observed (table 1). The frequency of inter-patch movement was higher in the fallow than in the wheat field (difference between two proportions: 22.7% in fallow and 6.25% in wheat field, P < 0.001). The two-way interactions of the factors of (1) field and movement and (2) recovery date and movement together best fitted the frequency distribution observed (maximum likelihood $\chi^2 = 9.764$, d.f. = 22, P = 0.988).

Table 1. *Marginal associations (chi-squared) and their probabilities (P) of field, sex, resight day and movement frequencies (log-linear analysis)*

Effect	d.f.	χ^2	P-value
Field	1	7.431	0.006
Sex	1	0.056	0.813
Resight date	3	21.086	< 0.001
Movement	1	128.304	< 0.001
Field × sex	1	0.995	0.318
Field × resight date	3	1.546	0.672
Field × movement	1	11.319	0.001
Sex × resight date	3	0.232	0.972
Sex × movement	1	0.780	0.377
Resight day × movement	3	12.231	0.007
Field × sex × resight day	3	1.934	0.586
Field × sex × movement	1	0.190	0.663
Field × resight day × movement	3	1.053	0.788
Sex × resight day × movement	3	0.148	0.985

3.3 Beetles' movement distance in relation to the factors studied

The overall mean 1-day movement distance was 0.309 m (range: 0–6.708 m, skewness: 4.148, fig. 2), and 1.942 m for non-staying beetles. The movement distance in the wheat (mean: 0.066 m) and in the fallow field (mean: 0.482 m) was significantly different (Mann–Whitney U-test: U = 7312.5, Z = −2.428, P = 0.015). The distance covered by non-staying beetles in wheat (mean: 1.058) and fallow field (mean: 2.114) was also significantly different (Mann–Whitney U-test: U = 53.5, Z = −2.385, P = 0.017). There was no significant difference between the movement of males (mean: 0.380 m) and females (0.241 m) (Mann–Whitney U-test: U = 8688.0, Z = −0.659, P = 0.510). The mean movement distances on the first, second, third and fourth experimental days increased (0.165, 0.216, 0.237 and 0.769, respectively) and proved to be significantly different (Kruskal–Wallis test: H = 13.573, d.f. = 3, P = 0.004). Multiple comparisons (non-parametric Tukey's test) showed that the contrast in the movement distances between the first and the fourth recovery events was responsible for the differences.

4 Discussion

4.1 Comparison of marking techniques

The results obtained in this study were in agreement with those previously published: bee markers with shellac were more persistent than paper labels (Caprio et al. 1990; Weber and Ferro 1994a). Although in the present experiment, bee marker was not perfectly persistent as reported in the study of Weber and Ferro (1994b), it worked well during the test (fig. 1). Consequently, it could be assumed that the vast majority of the decreasing recovery rate of beetles came from the beetles' movement, and not from the inadequateness of the marking technique.

4.2 Mid-season movement of the beetles

Literature data suggest that the density of vegetation negatively influences the movement activity of the CPB (Ng and Lashomb 1983; Weisz et al. 1994). Our results support this observation: the movement distance was significantly smaller in the wheat field than in the fallow field. Moreover, the frequency of inter-patch movements was reduced significantly in the wheat field (table 1). A possible explanation might be that the wheat provided a physical barrier to the beetle's motion, thus delaying their passage to another potato patch. However, a comparison of the proportions of inter-patch movements in wheat and fallow fields (the ratio of inter-patch movement in the fallow field was significantly higher than in wheat field) suggests that beetles respond to the contrast between the matrix of wheat and fallow field. In the fallow field visual and olfactory cues might more frequently trigger inter-patch movement than in the wheat field.

The most important finding of the present study was that mid-season movement of the beetles was rather limited. The majority of the beetles stayed in the same patch (84.1%). Although the present study examined the movement of beetles among isolated potato patches, our results are in agreement with the results of an experiment conducted in Michigan (USA) in which a great proportion of the beetles (71%) stayed on one plant during a 5-day experiment (Bach 1982). In case of newly emerged overwintered beetles, about 60% of the population stayed in the trap crop, and did not move from the overwintering site (woody border) to the potato field (Weber et al. 1994). This finding is in agreement with the field observation that CPB adults, especially newly emerged ones, are not always attracted to potato plants (Jermy and Sáringer 1955; Jermy et al. 1988; MacQuarrie and Boiteau 2003). The average distance of movement observed in this study was 0.309 m/day. This distance is much lower than the one that was observed for newly emerged overwintered beetles (Weber and Ferro 1994a). In the early season, the spring colonization of potato fields by the CPB proved to be more efficient if the distance between the previous year's planting and the present-day field was small (Lashomb and Ng 1984; Weisz et al. 1994). A distance of 0.3–0.9 km was sufficient to reduce a field's recruitment by the newly emerged beetles; however, according to the models fitted (Weisz et al. 1994; Follett et al. 1996), a perfect protection cannot be reached as at least a small proportion of the population is capable of colonizing fields from great distances (Boiteau et al. 2003). It is important to note that even if the average movement distance observed in mid-season was low, its range was rather wide. The limited movement activity in mid-season together with the observation that in the late season, the prediapause movement of the beetles is dominated by walking (Noronha and Cloutier 1999) suggest that the early season spring colonization of beetles is responsible for the fast dispersal of the beetle across the US and Europe (Boiteau et al. 2003). In the light of the present study, the great variability in movement distance and activity might also contribute to the dispersion of the CPB: it is capable of walking at approximately 1 cm/s (Thiery and Visser 1987; Jermy et al. 1988) a distance of several hundred metres and capable of flying even 100 km (Wiktelius 1981).

In the present study, the frequency of inter-patch movement (table 1) and the movement distances between male and female beetles were not significantly different. Similarly, Noronha and Cloutier (1999) did not find significant differences between the ratio of males and females in the traps both in the early and late seasons. In contrast, Weber and Ferro (1994a) found that males moved larger distances than females in spring and that the difference in the ability to fly or difference in the choice whether to fly or not led to the contrast in the movement distances of the sexes. The explanation of this phenomenon might be that the strategy of male the CPB is to maximize the number of matings with different females (Szentesi 1985), and mating status of the beetles might also influence their movement (Alyokhin and Ferro 1999).

We note that some factors might restrict the generalization of our results. For example, more than 40% of the beetles were not recovered, thus our conclusions were drawn only from a ratio of the beetles marked. According to our marking experiment, it is not very likely that more than 40% of the beetles lost their marker on the first experimental day. However, it is important to note that the greenhouse cage assay might have underestimated the number of beetles losing tags. Moreover, it is also not likely that we did not recognize a beetle on a plant although it was present. Another explanation is that missing beetles dispersed from the experimental area, as in a similar study in Massachusetts (Alyokhin and Ferro 1999).

In summary, our study demonstrated that mid-season movement of the CPB was limited (mean distance per day: 0.309 m). The significant difference in the frequency of inter-patch movements in fallow and wheat fields suggests that external factors (for instance, visual or chemical cues) could be responsible for the triggering of inter-patch movement. Results suggest that surrounding fields by wheat rather than fallow grounds should be studied as a possible strategy to reduce the movement of overwintered beetles between potato fields.

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