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The pattern, rate, and range of within-patch movement of a stem-galling fly

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Abstract. 1. Information on the movement of insects is critical to understanding the spatial spread, dynamics, and genetic structure of their populations, as well as their interactions with other species. With this in mind, the movement behaviour of the stem-galling fly *Eurosta solidaginis* Fitch (Diptera: Tephritidae) was investigated.

2. Fluorescent-marked adults were released at a single location within pure patches of the host plant, tall goldenrod *Solidago altissima*, and their distributions censused repeatedly throughout the day.

3. Following their release, male and female flies redistributed themselves in a manner that was well described by a simple-diffusion model. The diffusion rate was independent of fly density and time since flies were released.

4. Female flies dispersed at a significantly faster rate, and therefore farther on average, than males. Based on the diffusion model, it was estimated that at 2.5–3.0 h post release, males and females had a median dispersal distance of only 2.0 and 2.5 m respectively. Furthermore, 95% of the males were estimated to have dispersed no more than 5.9 m, and females no more than 6.4 m.

5. Post-release censuses suggested that flies were most active during mid morning, disappeared from the site at a rate of 10–15% per hour (most likely due to mortality), and survived for less than 2 days. Based on the rate of spread, diel activity, and liberal estimates of longevity in the field, 50% of the ovipositing females were predicted to have had a maximum lifetime range of movement within a patch of hosts of $\leqslant 51$ m (95% were expected to have been limited to $\leqslant 130$ m).

6. These data are used to assess whether the absence of a positive correlation between host-plant preference and offspring performance in this system could be due to the limited scale of dispersal of this species relative to the spatial scale at which its oviposition behaviour has been studied.

Key words. Diffusion model, *Eurosta solidaginis*, gall insect, goldenrod, mark–release experiment, movement, oviposition preference, preference–performance correlation, Tephritidae.

Introduction

Research over the past few decades has brought into clearer focus the role of movement in the evolution and ecology of insect populations. The pattern, rate, and range of movement are particularly important parameters because they can affect the spatial spread, dynamics, and genetic structure of populations, as well as interactions with other species (for recent reviews see Hanski & Gilpin, 1997; Tilman & Kareiva, 1997; Turchin, 1998; Bohonak, 1999). Quantitative data on movement have also proved valuable in developing management practices for pest species (Kennedy & Way, 1979; Stinner *et al*., 1983; Cronin *et al*., 1999).

Empirical studies of herbivore host-plant choice may also benefit from a knowledge of insect movement. A majority of studies on the subject has failed to support the expectation from simple evolutionary theory that natural selection should favour a positive correlation between host-plant preference and offspring performance (e.g. Karban & Courtney, 1987; Courtney & Kibota, 1990; Fox, 1993; Larsson *et al*., 1995;

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Craig *et al*., 1999). The absence of a correlation in field experiments may be a consequence of a limited range of dispersal in the herbivore. In particular, if the herbivore's range of movement is small relative to the size of the habitat under study, only a fraction of the individuals will encounter, and have the opportunity to choose, the most suitable host plants within that habitat. Thus, a positive correlation between host preference and herbivore performance may be obscured because of the incorrect choice of spatial scale. As studies of herbivore host-plant choice and offspring performance are taken outdoors (e.g. Anderson *et al*., 1989; Craig *et al*., 1999), the scale of herbivore movement will probably be of greater significance. To date, this has not been considered formally in most field studies of preference and performance.

Researchers have focused on the movement of organisms both among spatially discrete patches and within patches that are relatively homogeneous (for recent reviews, see Kareiva, 1990; Hanski & Gilpin, 1997; Tilman & Kareiva, 1997; Turchin, 1998). With regard to within-patch movements, which were the focus of this work, patterns of movement have often been found to be relatively simple: the redistribution of many insects is well described by a simple model of random diffusion (Kareiva, 1983, 1990; Turchin, 1998); however not all insect species exhibit within-patch movement patterns that can be modelled as such simple processes (see Kareiva, 1983; Turchin, 1998). For example, the redistributional patterns of some insects are better described by more complicated diffusion models such as those that allow for heterogeneous rates of dispersal within the population (Inoue, 1978; Okubo, 1980; Plant & Cunningham, 1991; Turchin, 1998; Cronin *et al*., 2000). Clearly, the patterns of within-patch movement cannot be assumed and must be ascertained experimentally.

In the work reported here, a mark–release experiment was used to quantify the pattern, rate, and range of movement of the stem-galling fly *Eurosta solidaginis* Fitch (Diptera: Tephritidae) within large homogeneous patches of its host, tall goldenrod *Solidago altissima* (Compositae). Through repeated, non-destructive, censuses of stem-galler distributions over time, this approach had the advantage of also being capable of estimating the loss rate of individuals during the course of the study (through death or disappearance). The within-patch redistribution patterns of male and female flies were tested against the prediction of a simple model of random diffusion. In addition, the diel activities, dispersal rates, loss rates, and lifetime range of movement of male and female flies were quantified. This work was motivated, in part, by a longstanding interest in the possible constraints influencing host-plant choice (reviewed by Abrahamson & Weis, 1997; see also Craig *et al*., 1999; Cronin & Abrahamson, 1999).

Methods

Natural history

Tall goldenrod is a long-lived perennial that propagates clonally through the production of rhizomes (How *et al*., 1994). Within recently disturbed fields, goldenrod clones often exist as discrete patches that are easy to distinguish (McCrea & Abrahamson, 1987; Anderson *et al*., 1989). As fields mature, however, clones introgress to form high density monospecific, but clonally diverse, patches of goldenrod (Abrahamson & Weis, 1997). The existence of extensive monospecific patches appears to be a relatively recent development in the history of tall goldenrod in North America. Prior to the immigration and spread of Europeans across the continent, tall goldenrod was probably much more sparsely distributed, primarily inhabiting river banks and naturally disturbed areas (Marks, 1983). Thus, the stem gallers have had a relatively short period of time to adapt to the current distribution of their host plant.

In the north-eastern United States, *E. solidaginis* adults emerge from within goldenrod patches in mid to late May (Uhler, 1951; Abrahamson & Weis, 1997). Males emerge first and await the arrival of females on the terminal buds of their host plant (Uhler, 1951; Craig *et al*., 1993). Immediately following mating, females oviposit preferentially into the buds of genetically susceptible, tall, and/or herbivore-free ramets (reviewed by Abrahamson & Weis, 1997; see also Horner & Abrahamson, 1999; Craig *et al*., 1999, 2000; Cronin & Abrahamson, 1999). Three weeks following oviposition, the stem tissue shows visible signs of swelling and by mid July the galls reach full size and are spheroid in shape (Uhler, 1951; Weis & Abrahamson, 1986; Abrahamson & Weis, 1997). The larvae overwinter in the third stadium within the galls, then pupate and eclose the following spring. Adults do not feed and can live approximately 7–10 days under optimal conditions in the laboratory (Uhler, 1951; Hess *et al*., 1996; Abrahamson & Weis, 1997).

Eurosta solidaginis *movement*

Experimental design. The pattern and range of within-patch movement of *E. solidaginis* was determined by marking adult flies with fluorescent powder, releasing them within the centres of monospecific patches dominated by goldenrod, and resighting marked individuals following dispersal. Adult flies were obtained from galls collected during the winter from fields near Bucknell University, Pennsylvania (40° 57′ 5.3″ N, 76° 51′ 53″ W). Galls were stored at –10 °C to maintain insects in diapause. To break diapause, galls were transferred to small screen cages placed within an environmental chamber at a constant 26 °C, 85% RH, LD 14 : 10 h photoperiod. Emerging adults were removed daily and stored in a separate growth chamber set at 10 °C (all other conditions identical). For this experiment, adult flies that had been in the cold growth chamber for 3–5 days were used. Flies experiencing this developmental regime show no detectable difference in oviposition behaviour from flies reared under natural conditions (Abrahamson & Weis, 1997; Cronin & Abrahamson, 1999).

In the evening prior to a mark–release trial, the thorax and abdomen of *E. solidaginis* adults were dusted lightly with fluorescent pigment (Dayglo Color Corporation, Cleveland, Ohio). Fluorescent pigments have been used previously to mark a variety of insect species, including bark beetles, fruit flies,

planthoppers, bees, and butterflies (Southwood, 1978; Kearns & Inouye, 1993; Turchin, 1998). At approximately 08.00 hours the next morning, small cup cages containing marked flies were placed on the ground within a 0.5-m diameter circle in the centre of a nearly monospecific patch of tall goldenrod. The lids of the cups were removed, but because of the cool temperatures at that early hour, insects remained on their perches within the cups. With the rising sun, flies slowly left the cups and began moving throughout the goldenrod patch.

At 30-min intervals, a team of two to five experimenters searched all vegetation above and below the goldenrod canopy for marked flies. Once a fly was discovered, experimenters recorded the time, sex, and behaviour (resting, mating, or ovipositing; behaviours were recorded only for trials 1 and 2) of the fly on a wire-stake flag, and the flag was placed in the ground next to the marked fly. The search for flies was terminated once a 30-m radius surrounding the release point had been inspected thoroughly (equal search effort was expended throughout this area). Approximately 15 min was needed to complete the search. In the first trial, the field was searched at 30-min intervals until dark (19.30 hours). The search for marked flies was resumed the next morning at 09.00 hours and finished at 15.00 hours. Because few marked flies were observed beyond 16.00 and 17.00 hours of the first day, all subsequent trials were terminated by 17.00 hours on the day of release. After each trial was complete, the distance from the centre of the release point and angle from magnetic north was measured and recorded for each flag. The flags were then collected for analysis of movement patterns.

Six mark–release trials were conducted. The first two trials were performed in spring 1997 in two areas at the Bucknell University Chillisquaque Creek Natural Area, 18 km NE of Lewisburg, Pennsylvania (Table 1). Although goldenrods were common throughout much of the 27-ha area, the experiments were conducted in regions that were nearly pure *S. altissima* ($\approx 3500\,m^2$ in area). The remaining four trials were conducted in spring 1998 within different regions of a single large old field 4 km NW of Danville, Pennsylvania. The entire field consisted predominantly of *S. altissima* and was ≈ 18 ha in size. All trials were conducted during the period when *E. solidaginis* adults were naturally emerging and searching for mates and oviposition sites. Trials were conducted on sunny days in light wind conditions (wind speeds $\approx 14\,km\,h^{-1}$).

One of the inherent constraints associated with mark–release experiments is that enough insects must be released to ensure that resighting frequencies are sufficient for statistical analyses. The release of insects at high densities can result in biased estimates of the rates or patterns of movement if movement is density dependent (Turchin, 1998). For example, at high release densities, insects may disperse more widely, or their movement paths may become more directed in order to reduce the frequency of intraspecific interactions. Conversely, insects in search of mates (particularly polygynous individuals such as *E. solidaginis* males) may become more sedentary in the presence of many prospective mates. To account for the possibility that release density affects fly movement patterns, the number of flies that was marked and released in each trial was varied from 10 to 450 individuals (Table 1).

Data analysis. The mark–release experiment was designed to obtain information on the density distribution of flies at fixed points in time, i.e. the different census periods. The simplest (null) model of movement involving the nearly instantaneous density distribution of marked organisms is based on the Gaussian or normal distribution (Awerbuch *et al*., 1979; Okubo, 1980; Turchin, 1998). In this model, N_r, the expected number of marked organisms observed at each distance, r, is determined by the following formula:

$$N_r = Ae^{-r^2/B}$$

Here, $A = \Phi N_0/4\pi Dt$, where Φ is a scaling parameter that is dependent upon resighting efficiency, N_0 is the number of marked organisms released, D is the diffusion rate, and t is the time since release. The parameter B is equal to $4Dt$. For this model, diffusion rate can be estimated directly from the distribution of recaptured organisms and is equal to the mean-square displacement of released individuals M divided by $4t$ (Kareiva, 1982, 1983; Turchin, 1998).

This model of diffusion assumes that drift, the directional bias in individual movement, is negligible among the released organisms (Turchin & Thoeny, 1993; Turchin, 1998). Prior to evaluating the diffusion model, drift among dispersing flies in each trial was tested by computing the mean x- and mean y-coordinates (x, $y = 0$ at the point of release) of resighted flies at the census period beginning 2.5 h post release (the period during which flies were resighted in highest numbers). Drift was determined to be significant if the 95% confidence intervals of the mean of these coordinates did not overlap the origin. In the event that drift was deemed important, the origin for that trial was recalibrated as the mean x- and mean y-coordinates from above (Turchin, 1998).

In the diffusion model, when dispersing organisms are sampled repeatedly over time, the diffusion rate for each time unit D_t is expected to remain constant (Kareiva, 1982, 1983; Turchin, 1998). This assumption was tested by computing the mean-square displacement of released individuals and the diffusion rate for each 30-min census period in a mark–release trial. A trend towards increasing or decreasing diffusion rates over time was evaluated by computing the Pearson's product-moment correlation R between the diffusion rate per census period and census period (Sokal & Rohlf, 1995). In the absence of a significant trend, the average diffusion rate $\bar{D}$ was computed. Differences in the average diffusion rate between male and female flies were assessed using a paired t-test and the effect of the number of flies released (natural-log transformed to homogenise variances) on the average diffusion rate was determined using the Pearson's product-moment correlation (separate tests for males and females).

The fit of the diffusion model to the density distribution of *E. solidaginis* was assessed in the following way. For each mark–release trial, resighted individuals were pooled into distance categories: 2-m wide annuli that radiated outward from the point of release (0–1.99 m, 2–3.99 m, etc.). The midpoint of these categories was used as the measure of r. By dividing the number resighted by the area of the annulus upon which r was based, the number of flies resighted per m^2 at each

Table 1. Mark–release–resight results from six experimental trials.

Trial	Date	Sex	Released	Diffusion rate ($\bar{D} \pm$ SE)†	Maximum resight distance (m)	D_t vs. t‡
1	28 May 1997	Male	150	0.91 ± 0.17	13.8	−0.15
		Female	300	1.60 ± 0.38	22.6	−0.12
		Both	450	1.38 ± 0.34		−0.10
2	6 June 1997	Male	100	0.34 ± 0.23	7.8	−0.58
		Female	150	0.78 ± 0.19	10.8	−0.71*
		Both	250	0.65 ± 0.15		−0.48
3	3 June 1998	Male	4	None resighted		
		Female	6	0.91 ± 0.20	3.3	0.44
		Both	10			
4	4 June 1998	Male	10	0.35 ± 0.06	4.5	0.43
		Female	15	0.70 ± 0.26	8.4	−0.10
		Both	25	0.67 ± 0.10		−0.03
5	4 June 1998	Male	25	0.25 ± 0.08	7.4	−0.08
		Female	25	0.47 ± 0.11	11.4	−0.05
		Both	50	0.37 ± 0.18		−0.11
6	5 June 1998	Male	50	0.71 ± 0.17	11.0	0.05
		Female	50	0.86 ± 0.29	13.0	0.44
		Both	100	0.85 ± 0.21		0.37

*Correlation is significant at $P < 0.05$.
†Based on the mean of the 30-min census periods D_t.
‡Pearson's product-moment correlation between D_t and time interval t.

distance category N_r was computed. The diffusion model described above has the linear form, $\ln(N_r) = \ln(A) - r^2/B$, and can be fitted using least-squares regression (Sokal & Rohlf, 1995). For estimates of N_r, only resighting data from the period of maximal resighting activity for each trial was used, in all cases the census period 2.5–3.0 h after the flies were released (approximately 10.30–11.00 hours). Because there were zero resightings at a few distances, 0.01 was added to each value of N_r before applying a natural-log transformation. Only for trials 1, 2, and 6 were there sufficient numbers of flies resighted during a census period to test the fit of the diffusion model. A separate regression analysis was performed for each trial and fly sex.

Estimates of the range of dispersal of male and female flies were based on the predictions of the simple-diffusion model. The estimates of A and B for trials 1, 2, and 6 were used to generate the expected Gaussian distribution of resighted flies (in two-dimensional space). From this distribution, the standard deviation σ and 50% ($=0.674\sigma$) and 95% ($=1.96\sigma$) quantiles were computed. These quantiles represent the radius of a circle r containing that proportion of marked flies. An estimate of the mean dispersal distance is unreliable because of the difficulty of predicting the tails of the Gaussian distribution accurately. Provided that D_t is invariant with respect to t (see Results), it is possible to extrapolate from the quantiles based on the census 2.5 h post release to daily dispersal distances.

The repeated censuses of the distribution of marked individuals following their release was used to quantify the loss rate of *E. solidaginis* within a patch of host plants. The loss of adult flies can be a consequence of death, long-range emigration, or disappearance below the goldenrod canopy. The loss rate L_t between successive census time intervals (30 min) was estimated as $1 - (C_{t+1}/C_t)$, where C is the census taken at time t or $t+1$. For each mark–release trial, least-squares regression was used to determine whether L_t was independent of time. Separate tests were performed for male and female flies. To assess whether male and female flies had different loss rates, the average loss for each sex within a trial was computed, then a paired t-test was performed on the averages among trials.

Marker effects on longevity

A potential problem associated with marking insects is that handling or marking insects may affect survival or dispersal ability. Data on the flight capabilities of flies with and without the fluorescent-pigment marker were impossible to obtain, however, given the minute amounts of pigment necessary to mark the flies, it is unlikely that this mark would reduce flight capability significantly. Alternatively, the small quantities of pigment may be toxic to the flies. A laboratory study was therefore performed to quantify the effects of this pigment on fly longevity. Eight potted goldenrod ramets 30–45 cm tall were established on a bench in the laboratory. Overhead lighting was provided by fluorescent bulbs and the room was maintained at a relatively constant temperature and humidity (mean of 22 °C, 45% RH). Each pot had a clear plastic tubular cage (20 cm diameter) with fine-screen lid inserted over the ramet. Three unmarked and three fluorescent-marked 1-day-old adult flies were added to each cage. Equal numbers of males and females were used for each treatment. Survivorship was monitored daily until all flies were dead, and difference in

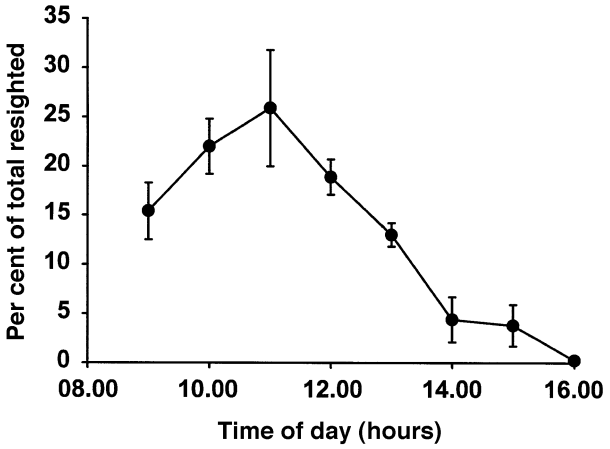

Fig. 1. Mean (± SE) percentage of the total number of resighted *Eurosta solidaginis* that were observed during the day of release (n = six trials).

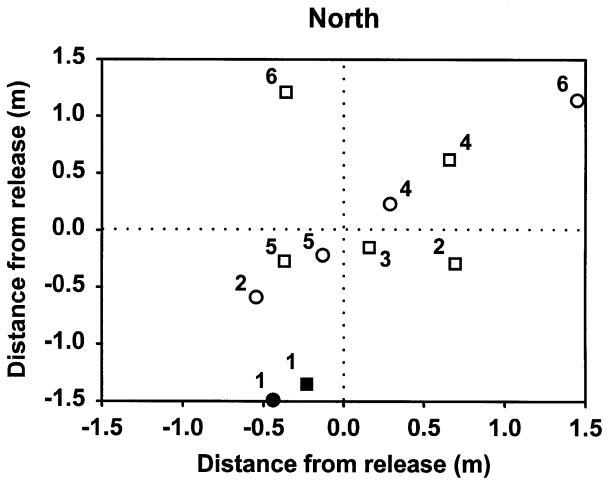

Fig. 2. Mean displacement of male (circles) and female (squares) flies 2.5–3.0 h following their release. Numbers associated with symbols indicate the mark–release trial and filled symbols denote a trial in which the 95% confidence intervals about the mean x- or y-coordinates do not overlap the origin (intersection of the dotted lines).

longevity between marked and unmarked flies was analysed using a two-sample t-test (Sokal & Rohlf, 1995).

Results

Eurosta solidaginis *movement*

Among the six trials of the mark–release experiment, flies were most likely to be observed during mid morning, with a peak resight frequency at around 11.00 hours (Fig. 1). Few marked insects were encountered between late afternoon (16.00 hours) and darkness. Flies were most commonly observed on the buds of goldenrods (40% of the resighted individuals), followed by goldenrod leaves (29%), non-host material (22%), and goldenrod stems (9%). For trials in which the behaviour of flies was observed (trials 1 and 2), 18% of the males and 13% of the females were engaged in mating, and 21% of the females were discovered ovipuncturing goldenrod buds. The range within which marked flies were observed to disperse in a day was relatively short: the maximum distance a fly was resighted was only 22.6 m (Table 1).

Drift of flies was absent in all but the first mark–release trial (Fig. 2). In that trial, there was a consistent but light breeze from the north that may have contributed to the southward displacement of male and female flies. To eliminate bias in movement, the means of the x- and y-coordinates were used as the origin for the release in trial 1 and dispersal distances were rescaled. This eliminated bias in the evaluation of the diffusion model (see below).

The within-patch diffusion rate estimated at each 30-min census period D_t did not increase or decrease significantly over the course of each day-long experiment. In only one of 12 cases, females in trial 2 ($R = -0.71$, $P < 0.05$), was there any evidence for an effect of time on the diffusion rate per census period (Table 1). Consequently, the diffusion rates per census period were averaged to produce the mean diffusion rate per trial $\bar{D}$ (Table 1). Despite very different numbers of flies released in each trial, there was no evidence of a significant change in the mean diffusion rate per trial as the number of marked insects increased, i.e. no density dependence in dispersal rate. For both males and females, the relationship between the mean diffusion rate per trial and the number of released flies was not significant (females: $R = 0.18$, P = NS, males: $R = 0.39$, P = NS), however female flies had a significantly higher mean rate of diffusion than males over all six trials ($\bar{D}_{\text{female}} = 0.89 \pm 0.16$, $\bar{D}_{\text{male}} = 0.51 \pm 0.13$; paired t-test, $t = 4.02$, $P < 0.05$, $n = 6$).

The pattern of redistribution of *E. solidaginis* was well described by a simple model of random diffusion (Table 2, Fig. 3). The fit of the diffusion model to the distribution of males with distance was statistically significant in all three trials, and provided an overall high coefficient of determination R^2 (average $R^2 = 0.85$, Table 2). The fit was not quite as close for females: in trial 1, the model provided a highly significant fit to the female's distribution-with-distance, but in the other two trials, the fit of the model was marginally nonsignificant (Table 2, Fig. 3). It should be noted that these latter trials were based on fewer numbers of released individuals, which could reduce the statistical power of these tests. Furthermore, an analysis of the residuals from these tests revealed no clear pattern in their distribution, thus a more complicated model of diffusion that included additional parameters and assumptions would probably not outweigh the advantages of this simple modelling approach. Dispersal quantiles, based on the predicted distribution of flies 2.5–3.0 h after release, are presented in Table 2. On average, 50% of males and females dispersed ⩽ 2.0 m and ⩽ 2.5 m respectively; the difference was not significant (paired t-test, $t = 1.68$, P = NS, $n = 3$). In comparison, 95% of the male and female flies were predicted

Table 2. Fit of diffusion model to resight data (2.5–3.0 h post release) for three replicate trials. The coefficients of determination R^2 and associated P-values are also presented for the diffusion model, along with the dispersal quantiles (radius of a circle enclosing the specified percentage of dispersers) for each sex.

				Dispersal quantiles (m)	
Trial	Sex	R^2	P	50%	95%
1	Male	0.88	0.019	1.93	5.61
	Female	0.92	0.009	2.04	5.92
2	Male	0.91	0.011	1.88	5.47
	Female	0.68	0.087	2.17	6.30
6	Male	0.77	0.050	2.31	6.72
	Female	0.72	0.069	2.41	7.00
Mean ± SE	Male	0.85 ± 0.04	0.027 ± 0.012	2.04 ± 0.13	5.93 ± 0.40
	Female	0.77 ± 0.07	0.055 ± 0.024	2.50 ± 0.23	6.41 ± 0.32

to have dispersed ⩽ 5.9 m and ⩽ 6.4 m respectively, during the same time period.

The average rate of loss of individuals (proportion/h) did not change significantly with time since flies were released. For each sex and trial, the least-squares regression of loss rate per census interval on census time t was not significant (for all comparisons, P = NS). On average across trials, the loss rates were 0.10 ± 0.04 and 0.15 ± 0.05 for males and females respectively. There were no sex-related differences in the loss rate ($t = 1.10$, P = NS, $n = 5$).

Marker effects on longevity

Adult flies that were handled and marked with fluorescent pigment did not live a shorter time than unmarked flies. Mean ± SE longevity in the laboratory was 9.1 ± 0.7 and 9.9 ± 0.8 days for the marked and unmarked flies respectively ($t = 0.761$, d.f. = 45, P = NS). Furthermore, marked flies retained the fluorescent pigment throughout their lifetimes and were never observed preening the pigment from their bodies.

Discussion

The mark–release experiment revealed that *E. solidaginis* adults were primarily active during the morning of their release and had disappeared by late afternoon (8 h later; Fig. 1). The loss rate of individuals averaged 10–15% per hour during the course of the day-long experiments. Long-range emigration, disappearance below the goldenrod canopy, or death may have contributed to this high loss rate. There was no evidence to suggest that flies were undertaking long-range flights that carried them beyond the 30-m radius of the study area. Many movement events were observed and all involved short-distance flights (< 2 m) that took place within, or just above, the goldenrod canopy. Disappearance of flies into the understorey (still alive) also appears to be an unlikely explanation for the high loss rate. A search of one of the goldenrod fields at night using ultraviolet lights did not reveal the presence of any marked flies (K. Hyland and W. G. Abrahamson, unpublished), nor were more than a couple of marked insects resighted the next day after release. Observers did, however, witness a few flies held in the chelicerae of spiders. Predation and other causes of mortality are probably the source of high loss rates for adult *E. solidaginis*. It can be surmised from these studies that the 3–5-day-old adult *E. solidaginis* survived only 1, or at most 2, days following their release into the field.

Following their release in a homogeneous goldenrod patch, both male and female *E. solidaginis* redistributed themselves in accordance with the predictions of a random diffusion model. This suggests that their movements were largely the net result of a random walk through the patch (see Okubo, 1980; Turchin, 1998). On average, females were much more mobile than males based on their rates of diffusion (0.89 vs. 0.51) and median dispersal distances (2.5 vs. 2.0 m) after 2.5 h. Emerging male *E. solidaginis* are known to ascend nearby goldenrod stems where they wait for and display to female flies (Uhler, 1951). A high percentage of marked males (≈ 70%) was perched on buds or leaves high on the stem, and it is likely that their short-range diffusive movements reflect this behaviour. Females, on the other hand, are very selective in their choice of oviposition site, preferring to oviposit into the stems of taller, faster-growing, well-watered, and herbivore-free ramets (Anderson *et al*., 1989; Horner & Abrahamson, 1992, 1999; Abrahamson & Weis, 1997; Craig *et al*., 1999; Cronin & Abrahamson, 1999), and it is therefore expected that they would travel more widely in search of suitable hosts (see also Stein *et al*., 1994). If these insects are taking a random walk within a goldenrod patch, it would suggest that they are discriminating among available hosts via short range or tactile cues. Several experiments in the laboratory have indicated that female *E. solidaginis* use chemical cues obtained during contact with the host plant (Abrahamson *et al*., 1989, 1994; Abrahamson & Weis, 1997).

The within-patch movement of female *E. solidaginis* is relatively short: in a 2.5–3.0-h period of time, 50% of the flies moved ⩽ 2.5 m, while 95% of the flies moved ⩽ 6.4 m. Given

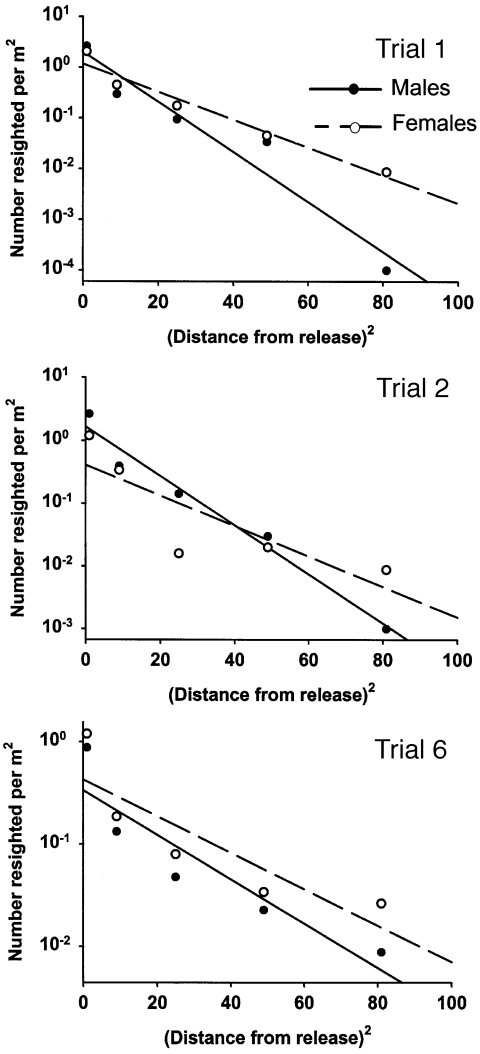

Fig. 3. *Eurosta solidaginis* resightings-with-distance for three trials (1, 2, and 6; see Table 1). The diffusion model predicts a linear relationship between the square of resighting distance and the logarithm of the density of resighted individuals. Lines are fitted by least-squares regression and are presented separately for males and females. Results are from individuals resighted between 2.5 and 3.0 h after release. The fit of the model to the data is presented in Table 2.

that females are active for ≤ 8 h per day and live as adults for probably no more than 7 days in the field (taking into account their age at release and their longevity following release), at least 50% of the females would be expected to have a maximum lifetime range of dispersal (net displacement from their origin) of no more than about 51 m, and 95% of the flies to have a maximum range no greater than 130 m. These distance estimates are based on the assumption that flies younger than 3–5 days of age are no more dispersive than the individuals released in these experiments. In nature, a single clone of *Solidago* spp. can span an area of up to 10 m in diameter (Werner *et al.*, 1980). Consequently, female *E. solidaginis* may not have the dispersal ability to reach and assess the chemical cues emitted from all of the available clones within a single field. This would be especially true for the fields within which this study was conducted; both were much larger than the area that could be covered by the large majority of female *E. solidaginis* in their lifetime.

Information on the lifetime range of movement of *E. solidaginis* can be used to evaluate one possible cause for the lack of a positive correlation between host-plant preference and offspring performance in field studies with this system: the range of stem-galler dispersal may not match the spatial scale of study. The goldenrod clones studied by Anderson *et al.* (1989) were distributed along an 8.2-km stretch of highway, so the spatial scale of this study greatly exceeded the distance that 95% of the ovipositing adult stem gallers would be expected to travel in their lifetimes. The summation of ovipositional activities of individuals that occur at relatively small spatial scales (< 130 m), across an area over 60 times larger, may obscure a positive correlation between preference and performance. Therefore, the absence of a positive correlation in the study by Anderson *et al.* (1989) may have been a consequence of an inappropriate choice of spatial scale. In two recent studies (Craig *et al.*, 1999; J. T. Cronin and W. G. Abrahamson, unpublished), the relationship between preference and performance was assessed in a 20×5 m common garden. The spatial dimensions of the garden were comparable in size to the range of movement of the stem galler, and both studies corroborated the findings of Anderson *et al.* (1989). These latter results suggest that the limited dispersal ability of *E. solidaginis* is not responsible for the absence of a positive preference–performance correlation in this system. The scale of movement of a herbivore should be considered when attempting to study the relationship between host-plant preference and herbivore performance in the field.

In the presence of a homogeneous, high density, patch of hosts, the rather short-range patterns of movement of *E. solidaginis* are to be expected, however a different pattern of movement may arise when stem gallers eclose as adults within a more heterogeneous, or coarse-grained, environment, as would be found in an early successional-stage old field. The ambit of movement of *E. solidaginis* may be much greater when moving among patches than within patches (McCrea & Abrahamson, 1987). In their study, a 0.5-ha goldenrod field isolated from any other source of goldenrods by ≈ 1 km was mowed early in the season to eliminate stem gallers. By the next fly generation the following spring, gall densities were at 63% of pre-mowed levels, suggesting that long-range dispersal across non-host habitat may be common in this species. Further studies are needed to understand the inter-patch movement behaviour of *E. solidaginis*.

Fruit flies in the family Tephritidae are important agricultural pests (Robinson & Hooper, 1989; White & Elson-Harris, 1992; Headrick & Goeden, 1998) and biological control agents of weeds (Harris, 1989; Julien, 1992; Turner, 1996). As a consequence of their economic importance, the movement and spatial spread of tephritids has received a proportionately high degree of attention relative to most other insect taxa. Most studies of tephritid movement have involved frugivorous

species (e.g. the Mediterranean fruit fly *Ceratitis capitata*), often following the introduction of irradiated adults (e.g. Plant & Cunningham, 1991; Vargas *et al*., 1995; Thomas & Loera-Gallardo, 1998). In contrast, fewer studies have attempted to quantify the movement patterns of gall-inducing tephritids (e.g. Varley, 1947; Jansson, 1991; Mays & Kot, 1996) or to study individual movement patterns (Jones *et al*., 1996). For those studies that have examined the redistribution patterns of tephritids, diffusion-based models have generally provided a good fit to the recapture data (e.g. Baker & Chan, 1991; Plant & Cunningham, 1991; Vargas *et al*., 1995; in some cases, a diffusion model more complicated than the one presented in this study provided a better fit). Given that the environments within which these studies were performed are much more complex than the goldenrod fields used in this study, it is somewhat surprising that the movement of these other tephritids can be reasonably well described by a diffusion process. It remains possible that a random walk, which would generate the patterns of redistribution in these studies (Okubo, 1980; Turchin, 1998), is a common feature of the family Tephritidae.

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