

Dispersal and foraging behaviour of *Platygaster californica*: hosts can't run, but they can hide

ANTHONY DARROUZET-NARDI¹, MARTHA F. HOOPES²,
JESSE D. WALKER³ and CHERYL J. BRIGGS⁴

¹Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado, U.S.A.; ²Department of Biological Sciences, Mount Holyoke College, South Hadley, Massachusetts, U.S.A.; ³Department of Biology, Utah State University, Logan, Utah, U.S.A.; ⁴Department of Integrative Biology, University of California, Berkeley, California, U.S.A.

Abstract. 1. Host–parasitoid models often identify foraging behaviour and dispersal distance as important for system persistence.

2. Laboratory observations and field trials were used to characterise foraging behaviour and dispersal capability of *Platygaster californica* Ashmead (Platygasteridae), a parasitoid of the gall midge *Rhopalomyia californica* Felt (Cecidomyiidae).

3. Although foraging parasitoids meticulously searched plants in laboratory observations, none of the laboratory trials resulted in 100% parasitism, and the proportion of parasitism declined as midge egg density increased.

4. The field trials showed that the distribution of parasitism over distance from a central release point was hump-shaped, as predicted by a simple diffusion model. Mean parasitoid dispersal distance was 4.5 m, considerably farther than the 1.7 m mean midge dispersal found in previous work.

5. Although the parasitoid appears to search thoroughly for midge eggs and to disperse farther than the midge, the results of this study show how this host–parasitoid system may persist due to spatially variable incomplete parasitism.

Key words. Gall midge, host–parasitoid interaction, inverse density dependence, persistence, *Rhopalomyia californica*.

Introduction

Research on parasitoids has proven indispensable in developing ecological theory about competition and predation (Hassell, 2000; Hochberg & Ives, 2000; Murdoch *et al.*, 2003) and useful in implementing biological control of insect pests (Murdoch *et al.*, 1985; Mills & Getz, 1996; Hawkins & Cornell, 1999). Hymenopteran parasitoids suppress populations of herbivorous host insects in many terrestrial biological systems. Knowledge of trophic dynamics, biodiversity, and evolution in these systems depends on understanding host–parasitoid interactions (Price *et al.*, 1980; Hawkins & Sheehan, 1994). In explaining the persistence of host–parasitoid interactions, mathematical models have supplied fundamental insights (e.g. Hassell, 2000;

Murdoch *et al.*, 2003). The models have emphasised the importance of density dependence and low levels of dispersal in persistent spatially distributed communities (Hassell *et al.*, 1991; Comins *et al.*, 1992; Briggs & Hoopes, 2004). Foraging and oviposition behaviour are often key parameters (e.g. Hassell *et al.*, 1991; Hassell, 2000).

Mathematical models of host–parasitoid interactions find a range of stabilising and destabilising effects of dispersal. Outcomes of dispersal depend on model form, differences in dispersal between host and parasitoid, prey carrying capacities, and predator interference or spatial variability in percentage parasitism (Murdoch *et al.*, 2003; Briggs & Hoopes, 2004). In general, high predator dispersal and attack rates coupled with strong differences in dispersal ability are destabilising (e.g. Crowley, 1981; Reeve, 1988; Rohani *et al.*, 1996) unless the prey has a partial refuge that creates a form of spatial density dependence to stabilise the interaction (Holt & Hassell, 1993). Spatial patterning resulting from the spatial interaction can lead to temporary spatial refuges, which can be stabilising (McCauley *et al.*, 1996;

Correspondence: Anthony Darrouzet-Nardi, Ecology and Evolutionary Biology, University of Colorado at Boulder, N122 Ramaley, 334 UCB, Boulder, CO 80309-0334, U.S.A. E-mail: anthony@darrouzet-nardi.net

de Roos *et al.*, 1998). In these persistent interactions, spatial variation in parasitism rates can increase stability by allowing small populations of midges to survive while larger populations experience high parasitism (Hassell *et al.*, 1991). Spatial variation with limits to dispersal is important to persistence because it maintains asynchrony among patches of hosts and parasitoids and keeps a metacommunity, or conglomeration of host–parasitoid communities, from behaving like a single host–parasitoid patch of interacting hosts and parasitoids (Leibold *et al.*, 2004; Hoopes *et al.* 2005).

Because measuring dispersal and attack probabilities of small organisms in the field is difficult, empirical support for mathematical models that incorporate dispersal and foraging is scarce. Dispersal data are available for only a few parasitoid taxa (Taylor, 1991; Corbett & Rosenheim, 1996; Jones *et al.*, 1996). Though research on foraging and oviposition behaviour is more extensive and encompasses more taxa (e.g. van Alphen & Galis, 1983; Ives *et al.*, 1999; van Alphen *et al.*, 2003; Wang & Messing, 2003), dispersal and foraging data are rarely examined at the same time. To work toward filling this empirical gap, this study examines the role of dispersal, foraging behaviour, and density dependence in the persistence of a well-studied host–parasitoid system consisting of the gall-forming midges *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) that are parasitised by *Platygaster californica* Ashmead (Hymenoptera: Platygasteridae) (Force, 1974; Hopper, 1984; Briggs, 1993). Foraging behaviour of *P. californica* was observed under controlled laboratory conditions. Spatial parasitism patterns and dispersal capability of *P. californica* were evaluated with three separate field release trials.

Because *P. californica* lives for 5–11 days (Force, 1970) and is a visibly better flier than the midge, it is likely that the average parasitoid disperses her eggs over a radius greater than that of the midge. Female midges, during their 1-day mobile adult stage, have been shown to disperse eggs an average of 1.7 m from their natal site (Briggs & Latto, 2000). The dispersal distance of the parasitoid, *P. californica*, is quantified in this study by release trials. If this dispersal difference between the midge and parasitoid is substantial, several mechanisms may operate that allow midge populations to escape parasitism and allow the midge–parasitoid interaction to persist: (i) although midge populations in the field nearly always have parasitoids associated with them, long distance dispersal events could allow the midge to initiate populations in patches where parasitoids have not arrived; (ii) if parasitoids tend to overlook some plants or galls while foraging, then the host–parasitoid interaction can persist despite high exploitation because overlooked populations create a refuge for the midge host (Holt & Hassell, 1993); (iii) if the number of parasitoid individuals that emerge from each gall or plant is constant, then there is inverse density-dependent movement of parasitoids into patches of midge hosts, leaving more midges to survive in galls or plants with high midge densities than in those with low densities. This type of inverse density dependence can be destabilising if it allows midges to escape from parasitoid control, but it can be stabilising under high parasitism pressure when it leaves the midge a partial refuge (Sih, 1987). Both the laboratory observations and the field release trials are used to provide insight on whether these mechanisms are operating in this host–parasitoid system.

Materials and methods

Study system

Platygaster californica is one of the most common of six parasitoids that attack the gall midge *R. californica* (Force, 1974; Hopper, 1984; Briggs, 1993). The midge forms galls on *Baccharis pilularis* De Candolle (Asteraceae), a common native shrub in coastal California. Galls are less than 1 cm in diameter and can contain over 100 developing midge larvae. While a suite of parasitoids attacks the midge larvae in the gall, *P. californica* is the only parasitoid that attacks midge eggs. *Platygaster californica* is a solitary parasitoid and a specialist on the midge (Ehler & Kinsey, 1991). Adult females are 1–2 mm in length. Caging experiments show that without parasitoids, the midge can outbreak and kill *B. pilularis* plants (Briggs, 1993); however, parasitoids are usually present, and midge outbreaks are rare under natural conditions (Ehler & Kinsey, 1991). Extremely isolated *B. pilularis* plants frequently have galls on them, suggesting that the midge dispersal curve is leptokurtic (see Kot *et al.*, 1996) and that parasitoid dispersal would have to be significantly higher than midge dispersal for parasitoids to find and exploit all midge populations. Parasitism of the midge tends to be over 70% and is frequently over 90% in the field (Briggs, 1993). Such high parasitism suggests that foraging *P. californica* females are extremely successful at finding and exploiting midge populations. More details on the natural history of *R. californica* and *P. californica* can be found in Briggs and Latto (2000).

Platygaster californica foraging observations

On-bush foraging conditions were simulated in the laboratory to determine how foraging time and percentage parasitism are related to the number of midge eggs present. Although they fly between *B. pilularis* bushes, *P. californica* females crawl to search individual branches for midge eggs.

On 27 June 2000, several hundred midge galls were collected from *B. pilularis* plants from Point Reyes National Seashore, Marin County, California, U.S.A. (38°2'N 122°53'W). The galls were kept indoors in a mesh-covered box at 22 °C. Midge and parasitoid individuals emerged each morning over the following 3 days between approximately 09.00 h and 11.00 h. Female midges were collected during the first day and placed in mesh sleeves on 14 potted *B. pilularis* seedlings, each about 20 cm tall. Having been left in the mesh-covered box with males for several hours, all females were likely mated. Midges were left on the branches for a variable amount of time to create a distribution of egg densities. The eggs that had been laid were then counted with a 10 × hand lens. Densities ranged from 0 to 132 eggs per plant. Previous research (C.J. Briggs and M.F. Hoopes, pers. obs.) suggests that only plants with midge outbreaks contained more than 132 eggs per branch tip; thus, this trial included a realistic high end of the distribution of egg density.

Platygaster californica females that emerged from the same galls were also collected. Their landings on a *B. pilularis* branch

were simulated by allowing them to crawl out of collecting vials on to leaves. The time that each female parasitoid spent on the *B. pilularis* seedling before flying away was recorded. This included the time the female spent searching for midge eggs and the time she spent probing midge eggs with the ovipositor. Galls were allowed to develop for 40–50 days in the greenhouse. The number of midge and parasitoid adults that developed in each gall were then counted. The galls were dissected to allow counting of the number of chambers occupied by midge or parasitoid larvae.

To look for density dependence in foraging time, the parasitoid search time per host egg was regressed against the natural log of the number of host eggs per plant ($\ln(\text{eggs} + 1)$). The host egg variable was transformed to improve the linearity of the regression. The parasitism rate (number of parasitoids that emerged per midge egg present) and the survival of midges were also regressed against the number of available host eggs.

Platygaster californica dispersal releases

Midge galls were collected at Point Reyes National Seashore in June, July, and August 2000 for three replicate trials. Female midges were released from these galls into lightweight polyester organandy mesh sleeves on the terminal 15 cm of *B. pilularis* seedlings (9–38 cm tall) that had been transplanted from the UC Berkeley Botanical Garden and grown in the greenhouse for several weeks. Each plant received one female midge. The mesh on the *B. pilularis* branches was left on to prevent any parasitoids in the greenhouse from parasitising the midge eggs.

All plants were visually inspected to make sure they had eggs on them before the plants were transported to the UC Berkeley Richmond Field Station in Richmond, California (37°92'N 122°34'W). In trials 1 and 3, the midge eggs were 0–3 days old; in trial 2, the midge eggs were 0–8 days old. Although some of the eggs in the second trial had hatched, the midge larvae were still vulnerable to *P. californica* attack because they had not yet burrowed into the meristematic plant tissue. *Platygaster californica* females can lay eggs in midge larvae until the midges burrow into *B. pilularis* tips to stimulate gall formation (Briggs & Latto, 1996). For each trial, potted *B. pilularis* seedlings were set up in five concentric rings in a large open field at the Richmond Field Station. *Platygaster californica* individuals were released from the centre of the array (Fig. 1, Experimental Design). The rings were 0.75, 1.5, 3, 6, and 12 m in radius. Although dispersing parasitoids could move from ring to ring in a stepping-stone fashion, each successive step doubled the step size. Thus, to reach the outer circle, a parasitoid had to fly a minimum of 6 m from the next smallest ring of plants. *B. pilularis* density was kept constant in each ring. Pots were spaced ≈ 2.4 m apart around each concentric circle. Thus, there were two *B. pilularis* plants at 0.75 m from the release point, four plants at 1.5 m, eight plants at 3 m, 16 plants at 6 m, and 32 plants at 12 m. This design prevented parasitoid females from preferentially parasitising the inner rings simply because they had a higher density of *B. pilularis* plants.

Three replicate releases were performed on 13 July 2000, 27 July 2000, and 10 August 2000. Before the releases, the entire

Richmond Field Station was searched for *B. pilularis* plants and the few small individuals that were found were removed. Male and female *P. californica* individuals were released to allow females to be fertilised (release 1: 96 females, 84 males; release 2: 74 females, 63 males; release 3: 103 females, 92 males). These parasitoid individuals emerged from the same collections of galls from which the midges emerged. Until release, the parasitoids were kept in small glass vials (one parasitoid per vial) at 10 °C with a drop of diluted honey for food. The parasitoid individuals were allowed to search for midge eggs for 4 or 5 days in the field. After that, the plants were moved back to the greenhouse where galls developed for 40–50 days inside mesh sleeves. The mature galls were dissected and the number of midge larvae as well as the number of parasitoid larvae in each gall were counted.

To assess parasitoid dispersal in the field trials, the proportion of plants, galls, and chambers with parasitoids were plotted against distance from the release point. At the chamber level, the experimental mean dispersal distance was calculated as the sum of the distance of all chambers from the release point divided by the total number of chambers, in order to compare with midge dispersal from previous work. Chamber counts were first normalised to account for differences in sampling effort at different distances. Because parasitoid egg numbers and distribution are limited by midge egg distribution, the data are contingent upon midge egg availability and cannot be analysed as straight counts. A Pearson χ^2 and Likelihood Ratio χ^2 were used to determine whether the proportion of chambers occupied by parasitoids differs among distances. Two different approaches were then used to assess how distribution changed with distance. Using the proportional data, Cochran's Linear Trend was used to determine whether there is a trend with distance. The data were also fit to the predictions of two models, a negative exponential function, following the procedure used to determine host dispersal (Briggs & Latto, 2000) and a diffusion model. For the diffusion model, $y = \exp\{-x^2/d\}$, where x is the distance from the release point, y is the probability that a *P. californica* egg was found beyond distance x , and d describes the step size (distance²/time, in this case m²/4–5 days). To fit the models, we set the proportion of total parasitoids found at further distances equal to the probability that a parasitoid laid eggs past distance x . We fit each release and the pooled data for all three releases for each model.

Because the oversight of entire galls or entire plants with galls by foraging parasitoid females would allow small refuges for the midge, the proportion of galls and plants attacked by *P. californica* at each sampling distance were also examined. At both the gall scale and the plant scale, logistic regression was used to examine the effect of distance and midge egg density on the likelihood of parasitoid attack. Low parasitism and high midge survival in some areas may make up for high parasitism in other areas with midges from high survival areas rescuing populations of midges decimated by far-dispersing parasitoids (Chesson, 2000; Hoopes *et al.*, 2005).

For comparison with the foraging data, the frequency of parasitism was compared with the number of host eggs available. In the foraging experiment, host eggs were in one to several clumps on one bush for each experimental unit. For the

release data, the change of parasitism with change in host density in a single clump of host eggs (per gall) and on single bushes (per plant) was examined by regressing the proportion of chambers occupied by *P. californica* at each of these scales

against the total number of chambers found in dissection. The total chamber number represents the number of midge eggs available for parasitism. SYSTAT 7.0 was used for all analyses (Wilkinson, 1997).

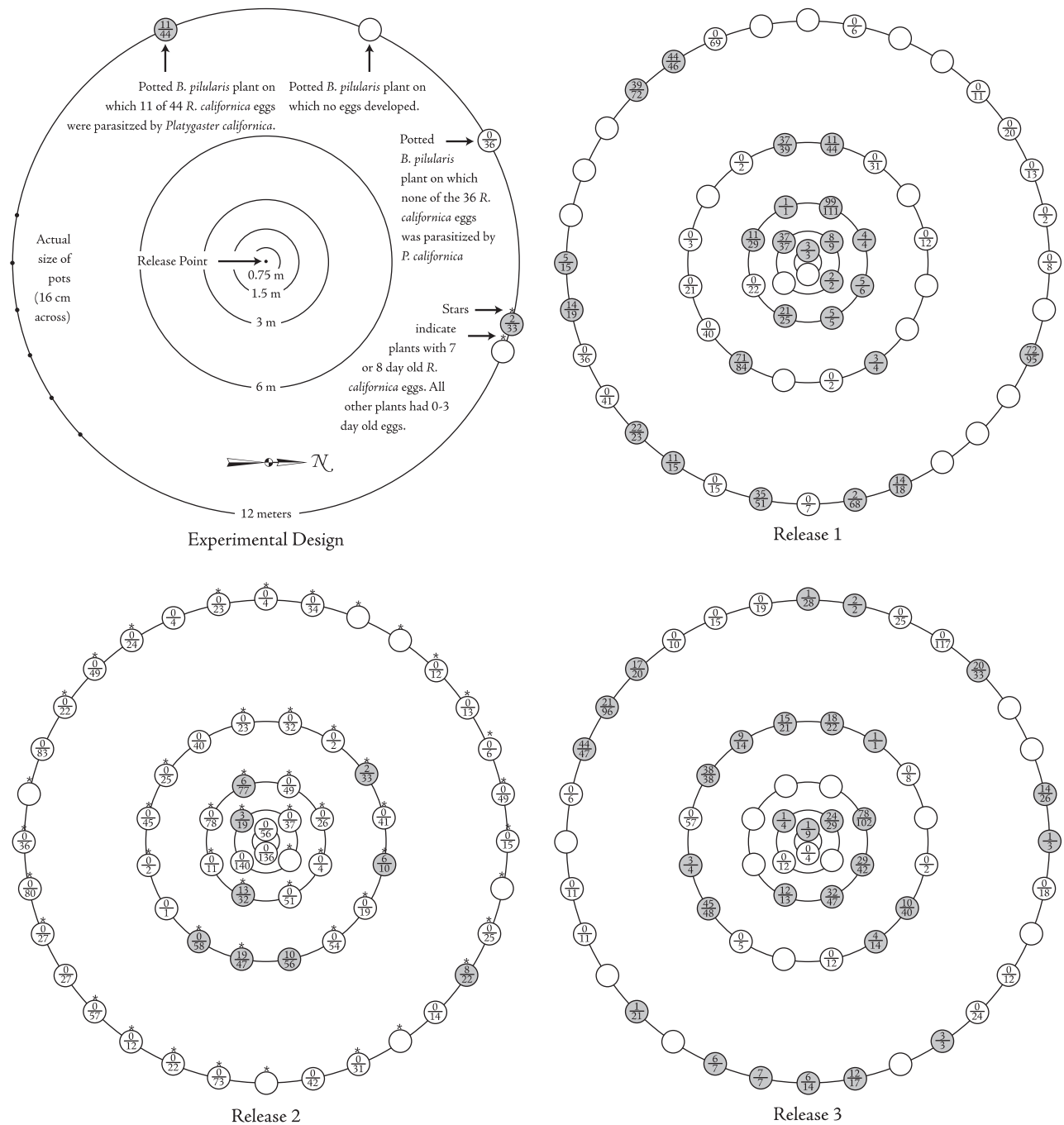


Fig. 1. Dispersal release field trials. Male and female *Platygaster californica* individuals were released from the centre of an array of potted *Baccharis pilularis* plants on three release dates. Each plant had *Rhopalomyia californica* eggs that were 0–3 or 7–8 days old. Some 7–8-day-old eggs had hatched; thus, they are marked by stars (only in release 2). Plants were left in the field for 4–5 days, and were then taken to the greenhouse where eggs developed. After 40–50 days, the galls were harvested and the fraction of the developed *R. californica* eggs that were parasitized by *P. californica* was determined; that fraction is displayed in the circles.

Results

Platygaster californica foraging observations

Negative density dependence was found in foraging time per host egg. In the foraging trial, the time per host egg that female *P. californica* individuals spent foraging declined as total host egg number increased (Fig. 2a; $n = 14$, $r^2 = 0.69$, standardised coefficient = -0.83 , $t = -5.18$, $P = 0.0002$). Strong inverse density dependence in foraging behaviour, however, was only marginally mirrored in actual parasitism rates. The regression of proportion of eggs parasitised against the total number of available midge eggs was not significant (Fig. 2b; $n = 11$, $r^2 = 0.30$, standardised coefficient = -0.55 , $t = -1.99$, $P = 0.08$), and this decrease in parasitism did not translate into an increase in midge survival. There was no significant relationship between the probability of survival for an individual midge and original midge egg density (regression $n = 11$, $r^2 = 0.06$, standardised coefficient = 0.24 , $t = 0.86$, $P > 0.4$).

Platygaster californica dispersal releases

In each release, *P. californica* was found to parasitise midge eggs up to 12 m from the release point (Fig. 1). The mean distance at which *P. californica* was found in the next generation was 4.51 ± 0.35 m from the release point for all releases taken together. No release differed significantly from this mean dispersal (4.57 ± 0.53 , 4.41 ± 0.90 , 4.46 ± 0.51 , mean ± 1 SE for release 1, 2, and 3 respectively).

At all scales – chamber, gall, and plant – parasitism by *P. californica* declined with distance from the release point. Looking at the total number of chambers across all three releases, χ^2 analyses showed a non-random frequency of chambers occupied by *P. californica* across distance (Likelihood ratio $\chi^2 = 62.99$, d.f. = 4, Pearson's $\chi^2 = 49.96$, d.f. = 4, $P < 0.00001$ for both), and Cochran's Linear Trend showed a significant decline in frequency of *P. californica* with distance (Cochran $\chi^2 = 12.82$, d.f. = 1, $P = 0.0003$). Cochran's Linear Trend tests whether the slope of a regression line through the proportions is significantly different from zero. The actual proportion of midge eggs parasitised by *P. californica* varied with release. All three releases showed a more hump-shaped than linear relationship between parasitism and distance although the hump in release 1 was close to the point of release (Fig. 3a).

This pattern is consistent with diffusion from a release point. The probability of moving past a particular distance declines with distance, but the probability of moving into successively further rings increases then decreases with distance. Each release had a significant fit to both the negative exponential and the simple diffusion model, although the fit to the diffusion model was slightly better (Table 1, Fig. 4). In Fig. 4 the proportion of total parasitoids found at each distance for each release is plotted. To attain the equivalent data from the model, the proportion of parasitoids at each distance (in each ring) was assumed to be equivalent to those parasitoids that made it past distance x_{i-1} but not past distance x_i . These assumptions are similar to assumptions made in mark-recapture models and in estimates of species spread (e.g. Andow *et al.*, 1990). The negative exponential model estimated mean distance of eggs from the release point as 3.8 m, 3.6 m, 4.0 m, and 3.7 m for all releases pooled and release 1 through 3 respectively. The diffusion model estimated mean distance of eggs from the release point as 2.8 m, 2.6 m, 3.1 m, and 2.7 m for all releases pooled and release 1 through 3 respectively. The proportion of galls and plants with at least one chamber occupied by *P. californica*, that is, with at least one parasitised midge, also declined with distance, although the relationship was not significant for each release (Fig. 3b,c; Table 1).

Density dependence in parasitism frequency at both the gall and plant scale was examined by regressing the proportion of parasitised chambers against the total number of chambers. Chambers represent both parasitised and unparasitised midge eggs whose larvae helped create a gall. At neither scale did these regressions reveal any significant density dependence or inverse density dependence for any release ($P > 0.05$). When the number of chambers was added to logistic regressions, host egg density did have a significant effect on whether or not galls or plants experienced any parasitism, but only in the first release (Table 2).

Discussion

The results from the foraging and release trials suggest that the parasitoid, *P. californica*, can move substantially farther than its midge host, *R. californica* (≈ 4.5 m from data or 3.0 m from diffusion models vs. ≈ 1.7 m), and that female parasitoids tend to search meticulously for midge eggs once landing on *B. pilularis* plants. These characteristics could lead to a highly

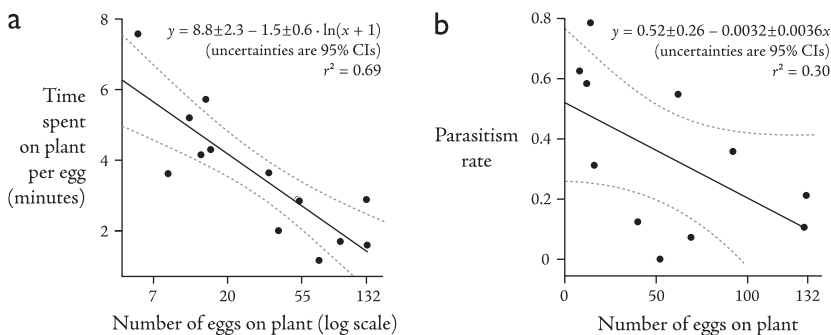


Fig. 2. (a) Foraging time per host vs. the natural log of available hosts. (b) Parasitism probability per host vs. the number of available hosts.

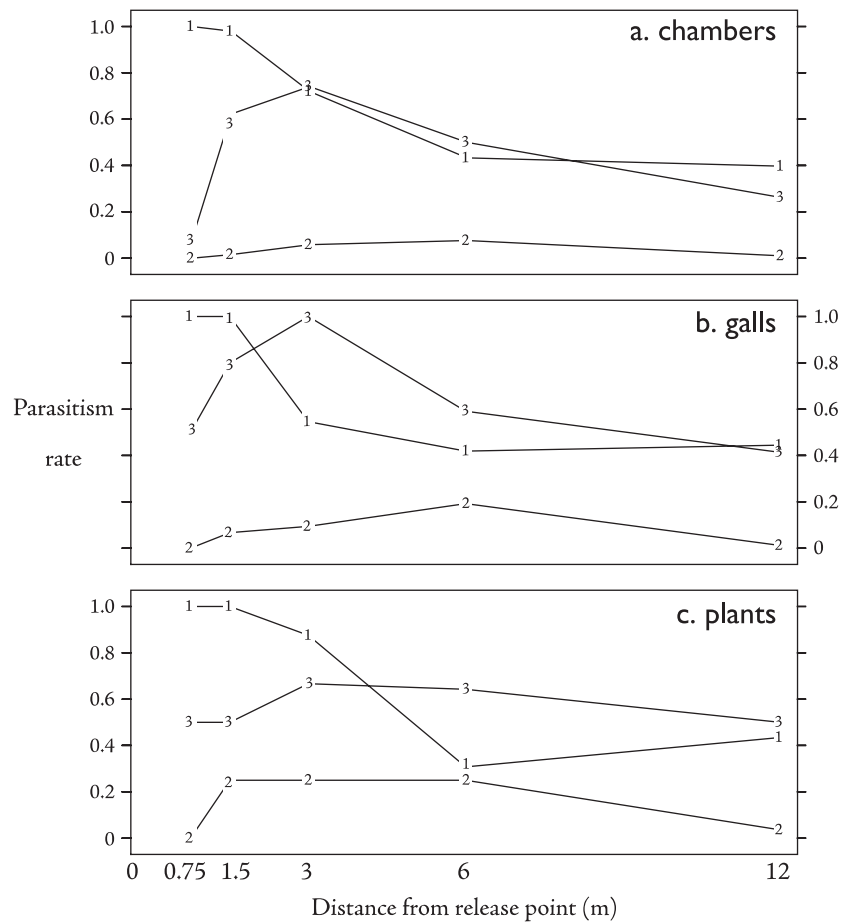


Fig. 3. Fraction of (a) chambers, (b) galls, and (c) plants that were parasitised by distance from the release point for each of the three releases. Release number is shown as plotting character.

unstable interaction, but in the field *P. californica* is one of the most common predators of the midge, and midge galls are found in almost all communities with *B. pilularis*. This high persistence may be explained by many factors outside the scope of this study, including seasonal or spatial variation that were not examined or interference from other parasitoid competitors, but it may also be explained by the high variation in parasitism probability that was found at several scales.

In the laboratory observations of *P. californica* foraging behaviour, parasitoid females found each cluster of midge eggs and appeared to probe each egg. Despite this observation and the absence of other distracting factors, such as predators or inclement weather, many midge eggs developed into adults either without being parasitised or having resisted parasitism. Marginal evidence of inverse density dependence was found in parasitism rates, meaning that parasitoids were less effective when the cluster of midge eggs was larger, but this change in parasitism rates did not translate into a change in midge survival. Three possible explanations are proposed for why midge mortality did not match the observed parasitism foraging behaviour. (i) The simplest explanation is that parasitoids may have missed single eggs or not been able to access eggs at the bottom of clusters. These omissions may not have been noticed during the foraging observations. (ii) *Platygaster californica* is known to be an egg-limited parasitoid, meaning that females are born with a limited

number of eggs and cannot create more during their adult life (J. Rosenheim, pers. comm.). Parasitoid females may not have enough eggs to parasitise every host they encounter. Too many eggs oviposited in a single cluster of hosts may reduce the parasitoid's fitness (Getz & Mills, 1996; Heimpel *et al.*, 1996, 1998; Casas *et al.*, 2000). A strategy in which females spread their eggs over more clusters would lead to lower parasitism rates in samples with more host eggs. Such a strategy would not preclude parasitoids from probing hosts in which they did not oviposit if such probes identified superior hosts or removed the

Table 1. Negative exponential and diffusion model fits to the data

	<i>d</i>	<i>R</i> ²	<i>P</i>
Negative exponential $y = \exp(-x/d)$			
All releases pooled	3.76	0.96	< 0.0001
Release 1	3.56	0.97	0.04
Release 2	3.98	0.97	0.04
Release 3	3.72	0.97	0.04
Diffusion model $y = \exp(-x^2/d)$			
All releases pooled	9.96	0.98	< 0.00005
Release 1	8.30	0.97	0.003
Release 2	11.97	0.99	0.004
Release 3	9.44	0.99	0.003

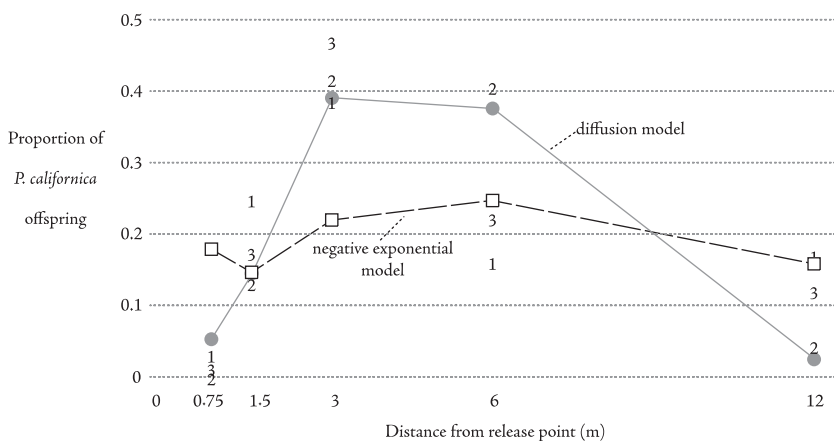


Fig. 4. The fit of diffusion and negative exponential models to the release data. The vertical axis shows the proportion of the total number of parasitoid larvae found at each distance. Release number is shown as plotting character.

host resource from competitors (Bronstein, 1988). (iii) Some midge eggs may rid themselves of parasitoid eggs immunologically. Studies have found such immune responses in other host insects (Strand & Pech, 1995).

In the field experiment, the dispersal ability of *P. californica* per generation exceeded that of its host. Briggs and Latto (2000) found that the mean midge dispersal in one generation was 1.7 m, and that no discernible midge galls developed beyond 7 m from the central release point; a mean dispersal distance for *P. californica* of 4.5 m (≈ 2.6 times as far) was found from data, and a mean dispersal of ≈ 3.1 m and 2.8 m was predicted from fits to the negative exponential and diffusion models respectively. Notice that both models may have produced underestimates because they were fitted to data in which no eggs were found past 12 m. *B. pilularis* plants were set out to only 12 m because parasitoid dispersal was not expected to outpace midge

dispersal so substantially. Although the diffusion model fit slightly better, longer distance sampling would better demonstrate the true shape of the dispersal curve.

The data show that *P. californica* can find and parasitise midge eggs up to 12 m away (possibly using closer *B. pilularis* plants as stepping-stones), or up to 6 m away across open habitat. Given the parasitism levels seen in the 12 m ring of releases 1 and 3, *P. californica* can likely parasitise midge eggs significantly beyond 12 m. Previous research has found that wind can significantly affect parasitoid dispersal (Messing & Rabasse, 1995; Corbett & Rosenheim, 1996; Desouhant *et al.*, 2003), but wind did not seem to be a factor in these trials. Despite the daily on- and offshore winds from San Francisco Bay, the parasitoid was able to seek out and parasitise midge eggs in all compass directions.

The lower rates of parasitism in the second release highlight the importance of proper conditions for parasitism. The obvious difference between the second release and the other releases was the older age of the eggs. Briggs and Latto (1996) showed that *P. californica* has a higher parasitism rate in younger eggs, but that it was able to parasitise some older eggs. There was, however, no consistent difference in parasitism of older and younger eggs in the second release. It is also possible that an unmeasured environmental factor or weather anomaly affected parasitoid behaviour or that there was something anomalous about either the midge or parasitoid individuals used in the second release.

Despite careful foraging and long distance dispersal by *P. californica*, there are several possible explanations for the persistence of the interaction and escape of the midge from parasitism. First, parasitism probabilities were found to decline with distance from the release point, with whole galls and whole plants escaping detection by parasitoids. A spatial decline in parasitism suggests that leptokurtic midge dispersal may allow some midge populations to escape parasitism. Smaller spatial refuges may also be possible. Because midge females lay many eggs in a single sitting, their eggs are organised into small stacks. Eggs at the bottom of the stack may be in a spatial refuge from parasitism. Similar to other experiments with this system (Force & Moriarty, 1988), no evidence was found of inverse density dependence in parasitism in the field experiment to support this hypothesis, but a lack of density dependence could also allow a proportion of hosts to escape parasitism. The superior dispersal ability and meticulous

Table 2. Logistic regression results for parasitism of galls and individual plants

	Parameter	Coefficient	SE	<i>t</i> ratio	<i>P</i>
All releases					
Galls	distance	-0.073	0.023	-3.104	0.002
	host eggs	0.007	0.007	1.064	0.287
Plants	distance	-0.087	0.040	-2.179	0.029
	host eggs	0.007	0.006	1.289	0.197
Release 1					
Galls	distance	-0.082	0.043	-1.894	0.058
	host eggs	0.028	0.013	2.106	0.035
Plants	distance	-0.200	0.085	-2.354	0.019
	host eggs	0.028	0.012	2.326	0.020
Release 2					
Galls	distance	-0.138	0.069	-1.985	0.047
	host eggs	-0.001	0.017	-0.042	0.966
Plants	distance	-0.194	0.106	-1.837	0.066
	host eggs	-0.006	0.013	-0.491	0.623
Release 3					
Galls	distance	-0.200	0.048	-4.191	< 0.001
	host eggs	-0.016	0.017	0.944	0.345
Plants	distance	-0.047	0.068	-0.686	0.493
	host eggs	0.019	0.013	1.505	0.132

searching behaviour that was documented for *P. californica* help explain the high rates of parasitism of galling midge hosts observed in the field. This study demonstrates how incomplete parasitism and spatial variability in parasitism may contribute to the persistence of this host–parasitoid interaction.

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