

Patch Time Allocation by a Parasitoid: The Influence of Con-specifics, Host Abundance and Distance to the Patch

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Abstract Patch residence time is at the core of models of decision making by foragers living in patchy environments. We studied patch residence time (PRT) of *Ibalia leucospoides*, a parasitoid of the woodwasp *Sirex noctilio*, as assigned to 4 treatments (recent feeding and/or oviposition experience) foraging in an array of host-infested pine logs. We tested the effects of distance from release point, host abundance, and the number of con-specifics at the time of arrival, on patch (pine log) residence time. PRT depended on a combination of patch quality (number of hosts in a log) and distance from the release point. Neither the presence of con-specifics on the patch, prior exposure to hosts, nor feeding prior to the experiment affected the time spent on a patch. We conclude that PRT in *I. leucospoides* meets Marginal Value Theorem predictions qualitatively, overruling the effects recent oviposition experience, access to food and contact with conspecifics. These findings are in line with the reported pro-ovigeny in *I. leucospoides* as well as the strong spatial aggregation of hosts in the field.

Keywords Biological control · dispersal · foraging behaviour · *Ibalia leucospoides* · *Pinus contorta* · *Sirex noctilio*

Introduction

The amount of time a forager spends on a patch is a central focus of behavioural ecology and is at the core of models of animal foraging for patchily distributed

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resources (e.g.: Stephens and Charnov 1982; Kacelnik 1984; Wajnberg 2006). According to classical work, patch residence time (PRT) should be adjusted according to the relative quality of the patch and the between-patch travel time (Charnov 1976; Stephens and Krebs 1986). A forager should invest more time in high quality patches than in low quality patches. Patch time should also increase with travel time. More recent work has addressed factors other than patch quality and distance between patches that may contribute to PRT, such as competition (e.g.: Goubault et al. 2005). In the presence of competitors, foragers should leave a patch sooner if competition increases the rate of resource depletion (van Alphen 1988). However, if the competitors instead interfere with one another (Lair et al. 1984; Mitchell et al. 1990) then perhaps a forager should stay longer. The conflicting needs for food and hosts (Bernstein and Jervis 2008), and changes in behaviour due to information acquisition or learning also contribute to patch residence time (van Alphen and Bernstein 2008, van Nouhuys and Kaartinen 2008).

Parasitoids are insects that forage as adults for arthropod hosts in or upon which to lay eggs. Their young develop as parasites. Parasitoids are frequently used in studies of animal foraging behaviour for several reasons. Firstly, they are part of virtually all insect communities, and play an important role on the regulation of insect populations (Hawkins 1994). Secondly, successful oviposition by these insects correlates strongly with host foraging behaviour allowing a straightforward link between individual behaviour and fitness. Finally, parasitoids are of interest to biological control practitioners given their widespread use as natural enemies of agriculture and forestry pests (Greathead and Greathead 1992; Mills and Wajnberg 2008).

Ibalia leucospoides Hochenwarth (Hymenoptera, Ibalidae) is a solitary, koinobiont parasitoid of the woodwasp *Sirex noctilio* Boidin (Hymenoptera, Siricidae) (Spradbery 1977). *S. noctilio* is a primitive xylophagous insect (≈10–40 mm long) that attacks pine trees. Adult woodwasps are typically short lived (<15 days) and do not feed. Thus resources they use as adults are obtained and stored during the larval stage. Females lay eggs within tree cambium during the summer and larvae develop throughout the rest of the year, drilling galleries and feeding on decomposed wood and hyphae of the symbiotic fungus *Amylostereum aerolatum* (Coutts 1969). While native to Mediterranean Europe, over the last century it has invaded Australia, New Zealand, South Africa, South America and more recently North America (Madden 1988; Klasmer et al. 1997; Hoebeke et al. 2005). In most regions where *S. noctilio* has established, it has rapidly become the most important pest of pine tree forests, due to its outbreak population dynamics, which can cause severe tree mortality (Corley et al. 2007).

Ibalia leucospoides, a large cynipid parasitoid (≈16–17 mm long) is one of several bio-control agents adopted for pest management of woodwasp populations (Neuman and Minko 1981; Haugen and Underdown 1993; Hurley et al. 2007). The parasitoid, native to Europe and North America, was introduced into Australasia in the early sixties. Since, it has established throughout the invasion range of *S. noctilio*, mostly through accidental introductions, together with its host (Madden 1988). In field conditions and at pine stand scale, *I. leucospoides* may parasitize up to 40% of its hosts. The parasitoid attack eggs and first instar larvae of *S. noctilio*. It is endoparasitic until the third instar, at which time it becomes an ectoparasite. In

spite of the fact that *I. leucospoides* is generally reported as a successful control agent of *S. noctilio* (e.g., Kidd and Jervis 1996), some studies suggest that under some environmental conditions its regulatory role is secondary to that of other parasitoids (Taylor 1978; Corley et al. 2004; Corley and Bruzzone 2009).

Because of its applied importance there is growing research on *I. leucospoides*, primarily focused on foraging behaviour (e.g.: Fernández-Arhex and Corley 2005, 2010). It has been shown that *I. leucospoides* uses chemical information derived from the symbiotic fungus, to locate and quantify hosts within a tree (Madden 1968; Martínez et al. 2006). This parasitoid has a type III functional response to host density in a tree. A sigmoid or type III response indicates that as host density rises, parasitoid attacks initially accelerate due to the parasitoid becoming increasingly efficient at finding hosts at low densities but then levels off with increasing influence of handling time or satiation (Fernández-Arhex and Corley 2005).

We studied patch residence time of *I. leucospoides* in a semi-natural setting, simultaneously considering a set of variables likely to influence patch time allocation under field conditions. A large number of individuals was released and allowed to forage naturally within an array of host-infested pine logs located at different distances from the central release point. The wasps were observed over two days, passing the night inactive on the log they occupied at sundown. We tested the effects of distance from the release site, host abundance and the number of con-specifics at the time of arrival, on patch residence time per visit. By exposing the wasps to different treatments prior to their release, we also tested for the effects of previous experience with hosts and feeding experience on residence time.

Material and Methods

Insect Rearing and Experiment Preparation

The hosts and parasitoids were reared from pine (*Pinus contorta*) logs collected from several heavily attacked plantations located in NW Patagonia, Argentina. Once felled, trees were cut into 1 m-long logs and kept individually in locker-type cages under ambient indoor conditions until insect emergence occurred. Each morning newly emerged insects were collected from the cages and immediately placed in individual vials, and stored in a refrigerator at 5°C until use. Only females which were cold-stored less than 15 days (less than 50% reported life time in laboratory conditions, Fischbein unpub.data) were used in the experiments.

Once the required number of *I. leucospoides* females was obtained (100 individuals, see below), each was randomly assigned to one of 4 treatments. Each parasitoid was marked according to treatment, with an acrylic paint dot on the thorax immediately upon removing them from the refrigerator, and then placed in 30 cm³ plastic cages (Bugdorm, MegaView Science Co., Ltd) for the 48 h before the experiment. For the “*feeding experience*” treatment, half of the specimens were given access to food (30% honey: water solution) during the 48 h prior to the experiment whereas the remainder were kept under similar conditions, with only water. For the “*oviposition experience*” treatment, 25 individuals from each feeding treatment category were exposed, 24 hs before the experiment, to host rich logs until

they oviposited twice, which usually occurred within 1 h. The remaining 50 wasps were kept in cages without hosts. Thus, at the time of release there were 25 females fed and with oviposition experience, 25 fed but lacking exposure to hosts, 25 with oviposition experience but unfed and finally, 25 females with neither hosts nor food.

To obtain host infested logs for the experiment, we cut ‘clean’ logs and left them to dry at ambient temperature for 10 days. This was done to ensure appropriate wood moisture conditions for woodwasp oviposition. A complete array of 1 m logs (20 logs in total) was placed in a conservatory where 200 *S. noctilio* females were released for 24 h. While we were unable to accurately establish the number of eggs laid in a log, we could ascertain, through direct observation, whether a log had been successfully attacked by at least one (but frequently several) wasp. Logs were then housed inside a glasshouse (all wasps removed) for a 11 days to allow host development and growth of the symbiotic fungus *Amylostereum areolatum*, which provides important host location cues to foraging *I. leucospoides* (Martinez et al. 2006).

The Experiment

The experiment was carried out during the austral summer of 2005/2006. We placed host-rich logs in a radial array inside a basketball gymnasium (50×28 m). Logs were arranged in 4 radiating lines of five logs set 2.5 meters apart (Fig. 1). As we did not know the density of host larvae in each log, the logs were assigned randomly to positions within the array. The closed-in gymnasium conditions insured almost homogeneous temperature and lighting and minimized air currents.

We started the experiment by placing the cages of parasitoids (1 cage per treatment) in the centre of the array, and slowly removing the covers, allowing the parasitoids to exit, either by walking or flying. To avoid dispersal due to agitation they were kept chilled until release. A total of 100 parasitoids were released at 11 h.

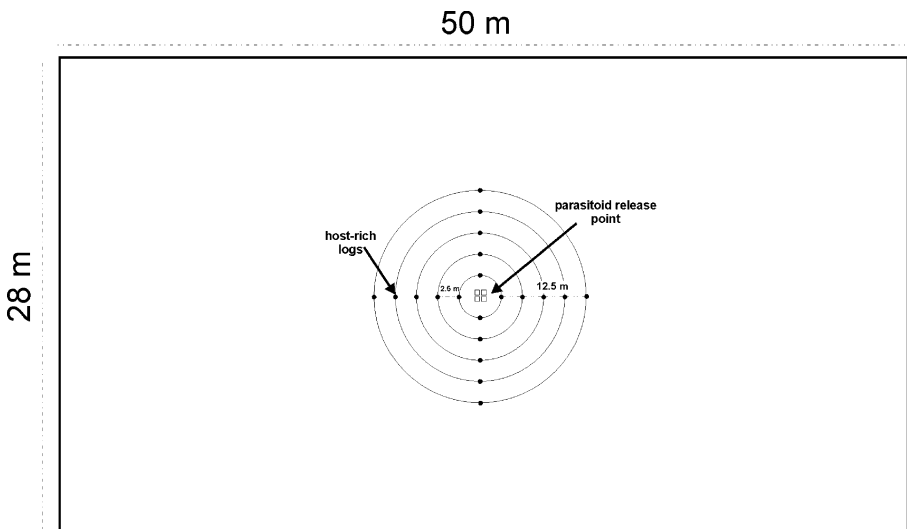


Fig. 1 Schematic representation of the experimental set-up, showing the spatial arrangement of the logs within the gymnasium

After release 4 observers walked slowly (to avoid agitation) along radial lines through the array systematically stopping to observe the wasps at each log. We recorded the identity (i.e.: treatment) of the wasps at each log. Patch residence time was measured as the amount of time that a focal individual was observed to be on a log. A focal individual was a wasp whose arrival and departure were both observed. The number of conspecifics is defined as the number of individuals upon arrival of the focal individual. The parasitoid observations were interrupted when the gymnasium became dark at night-fall (approx. 19 h), and were continued the following day, again until nightfall. All visited logs were removed after the experiment and housed individually in cages at room temperature so that all host and parasitoid emergences could be tallied after adult emergence the following season (2006/2007). This allowed an *a posteriori* estimation of the number of hosts per patch (by summing hosts and parasitoids emerged per log). We did not measure parasitoid emergence because, since multiple wasp visited each log, the rate of parasitism could not be attributed to individuals.

Data Analysis

To analyze the influence of *feeding status*, *oviposition experience*, *patch quality*, *patch distance* and the number of *conspecifics at the log* on *patch residence time*, we used a generalized linear model assuming a gamma distribution of residuals. The data were first fitted to an initial model and then, least significant variables were progressively removed from the model until a minimal appropriate model was obtained, in which all terms are significant. Single factors or variables incorporated into significant interactions were maintained in the minimum adequate model (Crawley 1993). The initial full model fitted to the data was patch residence time = distance of log*feeding treatment (either fed or unfed)*oviposition treatment (having attacked hosts or host deprived)* patch quality (host number on the patch)* number of con-specifics on the patch upon arrival; where * represents the sum of the influences of four-way, three-way and two-way interactions and the five single variables. All data analyses were done using the R statistical environment (R Development Core Team 2008).

Results

Twelve of 20 logs, distributed throughout the array, were visited by *I. leucospoides* (Table S1). In total 54 parasitoid visits were recorded, of which 51 allowed PRT observations. Thirty belonged to the unfed treatments (14 of these were of the “oviposition experience” treatment) whereas 21 belonged to the fed group. Among the latter, 9 visits to logs were by females allowed to oviposit on hosts before the experiment. The number of visits was not affected by either of the treatments studied ($\chi^2=0.07$, $p=0.79$; see also further analysis) and occurred mostly on logs closest to the release point. The remaining 49 *I. leucospoides* females dispersed out of the experimental array, landing and remaining on the gymnasium’s walls or ceiling. Three individuals that landed on a log but remained less than 15 min and did not attempt to oviposit were left out of PRT analyses.

The number of hosts per log varied between 4 and 124 (mean value=63.6). The maximum number of con-specifics observed on a given log upon focal parasitoid arrival was 13 whereas the minimum was 0 (mean value=4). A summary of host density, number of con-specifics, and distance of the log from the release point according to parasitoid visits is provided in Table S1.

Patch residence time (PRT) of *I. leucospoides* varied from 100 to 1759 min (mean=1164 SD 571). PRT was unrelated to wasp feeding status, prior experience or number of conspecifics at a patch. There was also not a simple association of PRT with the distance from the origin or patch quality (number of hosts present). According to the marginal value theorem we would expect wasps to make short visits to low quality patches which are at shorter distances, and make long visits to high quality patches, as well as those that take longer travel times to get to. We found that wasps tended to make long visits to rich patches (Table S1) near the origin (2.5 m from release point), while shorter visits became more common as patches decrease in host abundance (i.e.: logs with 22 hosts). In turn, for longer distances (≥ 5 m), patch visits are primarily longer, despite reported variability in patch quality (distance by quality interaction $F=8.4130$, $p=0.00565$; Fig. 2, Table 1).

Discussion

Patch residence time of female *I. leucospoides* on host-rich logs depends on the interaction of patch quality with patch distance. Overall, close to the release point the wasps visited both high and low quality patches. They made long visits primarily to logs with high host density or to those near the release point. Previous exposure of parasitoids to food or hosts (in which they oviposited) was unrelated to the amount of time they spent on a patch. Moreover, the presence con-specific foragers on the log did not modify PRT.

Theoretical work and several experimental studies have shown that competition among foraging parasitoids can modify patch use rules. Standing predictions propose a ‘war of attrition’ where foraging parasitoids should stay longer on a patch with competitors than when foraging alone (Beddington 1975; van Alphen and Vet 1986; Humphries et al. 2006; Goubault et al. 2007). Alternatively parasitoids should leave

Fig. 2 Patch residence time (y axis, minutes) of *Ibalia leucospoides* according to the significant explanatory variables: log location in terms of distance from the parasitoid release point (symbols) and host richness (x axis)

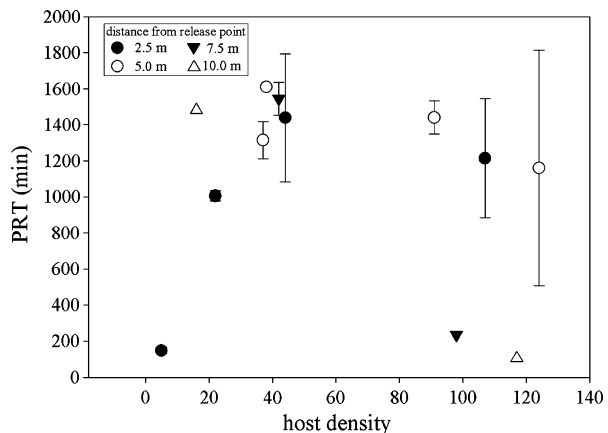


Table 1 Analysis of variance of the model $p_{rt} \sim dist + host + dist * host$ (gamma model, link function: inverse); terms added sequentially (first to last). Dependent variable: parasitoid patch residence time (PRT). Explanatory variables are distance from the release point at the centre of the array (*dist*) and the number of hosts in the log (*host*)

	d.f.	Deviance	Residuals d.f.	Resid. deviance	F	p-value
Null			50	28.9015		
Distance	1	0.0080	49	28.8934	0.0289	0.86583
Host	1	0.1103	48	28.7832	0.3973	0.531522
Distance*host	1	2.3180	47	26.4652	8.3529	0.005811

a patch earlier if their profit rate decreases because con-specific exploitation reduces the *per capita* profitability (Visser et al. 1990).

We found that PRT neither decreased nor increased with the presence of conspecifics. Even on logs where 13 females were present upon arrival of a focal insect, PRT was not significantly affected. This finding shows that information derived from con-specifics is either not perceived (note here that parasitoids did not visit patches prior to choosing) or else is unimportant. Recent related work on *I. leucospoides*, in which a pair of females was watched while foraging on logs of varying host densities also indicated that, while some interference competition may be noted, patch residence time is more affected by host density on a patch than by the presence of another individual on it (Fernández-Arhex and Corley 2010). This insensitivity to conspecifics suggests that interference competition is minimal, and that in their natural environment wasps may not be host limited at the scale of an infested tree.

Parasitoids, of course rely on host encounters for successful oviposition. However, as adults most species also forage for food in the form of nectar, and feeding can increase reproductive success by increasing egg production or longevity (Winkler et al. 2006; Bianchi and Wäckers 2008). But, the importance of feeding depends on the life history characteristics of the species as well as the age and nutritional status of the individuals (Jervis et al. 2008). Adult *I. leucospoides* females emerge with an almost complete load of mature eggs (ovigeny index close to 1; D. Fischbein, unpub. data). The lack of influence of feeding experience on PRT that we observed is in line with the high number of mature eggs (≈ 500) held by females *I. leucospoides* upon emergence (Fischbein et al, submitted).

Host deprivation and inexperience are other factors that could influence PRT. Indeed, several experimental studies have likened host deprivation to travel time (Thiel and Hoffmeister 2004). Similarly, parasitoids that have not experienced oviposition may forage less efficiently than those that have (Turlings et al. 1993). In our study, we found no effect of previous oviposition experience on PRT or dispersal. Either these wasps have strong innate foraging behaviours that are not easily altered by experience or experience did not have the appropriate timing or duration to trigger a change in behaviour (Smid et al. 2007).

Patch residence time predictions derived from the marginal value theorem (MVT) are contingent on a few assumptions. One is that foragers know the relative qualities

of the patches in a system, and the time it takes to get to each patch. Another assumption is that parasitoids forage alone. Despite the fact that these assumptions are unlikely to be met in nature, MVT predictions about patch residence time are often met by parasitoids (Wajnberg 2006).

Ibalia leucospoides may conform to the first assumption because it can detect patches (host infested trees) at a distance through airborne chemical cues derived from the growth the fungal symbiont associated with the host (Martinez et al. 2006). While foraging females did not visit and assess the quality of every patch, it is likely, given the chemical nature of patch attraction, that the parasitoids were more strongly attracted to the closer and richer logs. Most *I. leucospoides* females also functionally adhere to the second assumption, of foraging alone, since they appear to be unperturbed by the presence of conspecifics (see Fernández-Arhex and Corley 2010 for a more detailed study on conspecific interference).

Our findings show that patch residence time in *I. leucospoides* is determined by how many hosts are in a patch and by the distance travelled to get to it, qualitatively meeting the Marginal Value Theorem's predictions. In contrast to studies carried out on other parasitoids (see Wajnberg 2006 for a review), PRT was not modified by either the stimuli generated by recent oviposition experience, access to food, or even by the presence of other foragers on the patch.

Patch residence time is an important component of studies of predator-prey interactions and dynamics. It can also provide information useful for understanding success in biological control programs when pest species are spatially aggregated (Hassell 2000; Wajnberg 2006). Our experiments differ from past PRT studies (e.g.: van Alphen 1988; Vet et al. 1995) in that it involves a more natural scenario with multiple patches and multiple foragers. Parasitoids were allowed to move freely over a relatively large area for extended periods of time, and several behavioural processes were considered together (Thiel and Hoffmeister 2004 for another example).

Our main conclusion is that patch residence time in *I. leucospoides* is largely determined by the relative abundance and distribution of its hosts. For this parasitoid patches are highly aggregated and normally present in low numbers in the field. As noted in previous studies (Fernández-Arhex and Corley 2005; Corley et al. 2007), for females bearing a full egg-load upon emergence, finding host patches is a major constraint. Following individuals through longer time periods and evaluating individual oviposition are probably the next steps in this direction (e.g.: Cronin and Strong 1999; Tentelier et al. 2006).

Our experiments were designed to represent a natural scale host outbreak. Thus, all logs (\approx trees) bore hosts and some even had relatively high numbers of them. It is worth noting that even though many parasitoids visited several logs throughout the duration of the experiment (2 days), many logs received no parasitoid visits. While it is possible that the unvisited logs had very few hosts (unvisited logs were not stored for latter rearing), this seems unlikely because among the visited logs, even those with few hosts were visited by multiple wasps. These findings contribute to the accumulating evidence that *I. leucospoides* moves too little among infested trees, and may be of limited significance to overall woodwasp mortality (Corley and Bruzzone 2009). This is supported by the continued spread and outbreaks of *S. noctilio* populations where *I. leucospoides* has been introduced.

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