ORIGINAL ARTICLE

The effects of patch richness on con-specific interference in the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibaliidae)

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Abstract We experimentally studied con-specific interference in *Ibalia leucospoides*, a parasitoid of the woodwasp *Sirex noctilio*, on pine logs containing variable numbers of woodwasp larvae. Competiton occurred when two different-sized female parasitoids foraged on a host patch, and consequently the small female always abandoned the patch. Regardless of host density, con-specific presence did not affect the attack rate, the number of hosts attacked, nor patch residence time by the winner, when compared to a control female that foraged alone. In contrast, con-specific presence reduced patch time and the number of hosts attacked by the loser. Finally patch time (by both) as well as number of hosts attacked (by the winner only) increased with host density per patch. Our results suggest that con-specific presence has different consequences for different-sized females during patch exploitation.

Key words aggregation, direct competition, host–parasitoid interactions, parasitoid competition, patch quality, *Sirex noctilio*

Introduction

Parasitoid foraging behavior is known to be affected by the presence of con-specifics on host patches (Visser *et al.,* 1990; Hassell, 2000; Goubault *et al.*, 2007). Several parasitoid females exploiting the same host patch may interfere with each other, either directly as occurs for example through fighting or the display of specific hindering behaviors (Godfray, 1994), or indirectly by modifying host exploitation strategies (Visser *et al.*, 1990). Through con-specific interference between foraging females, host–parasitoid interactions may become more stable. This is a consequence of the decrease in individual attack rates when parasitoid density increases (van Alphen & Vet, 1986; Visser *et al.*, 1999). Still, the decrease in *per capita*

parasitism rates may have adverse effects on parasitoid growth and fecundity (Hassell & Varley, 1969; Kidds & Jervis, 1996; Hassell, 2000).

In heterogeneous systems, as most natural environments are, hosts tend to aggregate on resource-richer patches. The resulting spatial host distribution may, in turn, induce parasitoid aggregation, which may lead to an increase in individual encounters. Although parasitoid re-distribution and dispersion to other patches is likely to occur (Corley, 1999; Hassell, 2000), parasitoid congregations on a patch may promote con-specific interference.

The woodwasp *Sirex noctilio* Boidin (Hymenoptera: Siricidae) (Spradbery, 1977; Madden, 1981) is a primitive xylophagous insect that attack pine trees. While *S. noctilio* is native to Mediterranean Europe, in the last century it has successfully 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 a very important pest of pine tree afforestation, due to its reported outbreak population dynamics during which tree mortality can be severe (Corley *et al.*, 2007). Trees attacked by *S. noctilio* are spatially

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aggregated, especially during long-lasting endemic population phases, during which overall attack densities are typically low (Corley *et al.*, 2007).

Ibalia leucospoides Hochenwarth (Hymenoptera: Ibaliidae) is a solitary, koinobiont parasitoid of *S. noctilio*. This parasitoid is one of several bio-control agents adopted for pest management purposes of woodwasp populations (Neumann & Minko, 1981; Haugen *et al.*, 1990; Haugen & Underdowm, 1993; Hurley *et al.*, 2007). The parasitoid, also native to Europe, was introduced into Australasia in the early 1960s. Since then, it has established throughout the invasion range of *S. noctilio*, mostly through accidental introductions, together with its host (Rebuffo, 1980; Madden, 1988; Carvalho, 1993). The parasitoid attacks eggs and first instars larvae of woodwasps, and is endoparasitic until the third instar, a stage at which it becomes an ectoparasite. Its life cycle is closely related with the development of woodwasp larvae, usually lasting 1 year (but see Corley *et al.*, 2004).

In field conditions, *I. leucospoides* may parasitize up to 40% of its hosts, although values are highly variable in space and time (J.C. Corley, unpubl. data). In spite of the fact that *I. leucospoides* is generally reported as a successful control agent of *S. noctilio* (e.g. Kidds & Jervis, 1996), some studies suggest that under given environmental conditions its regulatory role is secondary to that of other parasitoids (Taylor, 1978; Corley & Bruzzone, 2009). Because of its applied importance there is a growing amount of research on *I. leucospoides*. Most work has focused on its foraging behavior (Chrystal, 1930; Madden, 1968; Spradbery, 1970a, b; Fernández-Arhex & Corley, 2005; Martinez *et al.*, 2006). It has been shown that *I. leucospoides* uses chemical information derived from a fungus, symbiotic of its host, to locate and quantify hosts within a tree (Madden, 1968; Spradbery, 1974; Martinez *et al.*, 2006). Also, this parasitoid has a type III functional response, determined to some extent by its ability in locating hosts at low densities (Fernández-Arhex & Corley, 2005). The mechanisms leading to low levels of parasitism still remain unknown, but con-specific interference could affect parasitism by this species.

In this work, we studied con-specific interference in the parasitoid *I. leucospoides* across different host densities. We did so through a series of laboratory experiments, using pine tree logs bearing different densities of *S. noctilio* eggs. Given the observed persistence of the host-parasitoid interaction and host strong spatial aggregation and low densities, our working hypothesis is that several *I. leucospoides* females on the same patch should compete. We consequently predict that for patches bearing two parasitoids, *per capita* attack rates should be lower (or else total attack numbers similar or lower) than on those visited by a single forager, irrespective of host abundance on the patch. Also, individual patch residence time displayed by competing foragers should be lower on poorer patches and for one of the competitors, as consequence of it abandoning the patch.

Materials and methods

Collection and rearing of hosts and parasitoids

Adult parasitoids were obtained from 1-m long lodgepole pine billets (*Pinus contorta* var. latifolia), collected in the field by logging attacked trees, in the proximity of Bariloche, Argentina (41°08′S; 71°20′W). Logs were kept under ambient conditions (24.4 ± 0.4°C) in locker-type cages, and checked on a daily basis during host and parasitoid emergence.

Preparation of host patches

Host-rich logs were obtained by releasing a single *S. noctilio* female on a clean, freshly cut 0.5 m-long *P. contorta* (log diameter varied between 9.5 and 11 cm). *S. noctilio* is a primitive, solitary wood-boring wasp whose larvae develop inside the xylem of pine trees. Successful host oviposition is difficult to ascertain for this species, because eggs are laid in tunnels within the wood that branch out from a single hole (number of eggs per hole, 0–3) (Madden, 1974). Therefore, we considered only holes in which the woodwasp had inserted its ovipositor completely, because these contained at least one egg and fungus (see Madden, 1968, 1974; Fernández-Arhex & Corley, 2005). We continuously observed host females until the desired number of holes was achieved, and marked each drill, which used a proxy of host density, with a white pen-eraser. The experiment started after 1 week of host drilling because then hosts are usually found as first instar larvae.

Experimental set-up

We simultaneously exposed two recently emerged female parasitoids (< 48 h) to the pine logs containing hosts. To distinguish the two females, one of them was marked on its thorax with acrylic paint before the trials (parasitoids were anaesthetized by placing them for 2 h at 5°C, to facilitate the marking). The experiments were carried out inside a wire mesh cage (1.0 × 0.4 m) at a temperature of 26.2 ± 0.2°C and natural midday lighting. Prior to the tests, parasitoids were housed individually for 24–48 h, with access to food (30% sucrose–water

solution) but host-deprived, in small plastic cages (30 cm^3) in closed room conditions (natural lighting and a temperature of 24.4 ± 0.4°C).

The experiment started when the two females were simultaneously placed on a log. We observed both parasitoids continuously, until they flew off to the cage walls and remained 'off-the-patch' for at least 5 min (end of experiment). Our response variables were the number of holes attacked and the total time on the patch per trial by the two parasitoids. We used a logistic regression model (Hardy & Field, 1998) to evaluate if the first parasitoid that abandoned the log had a relationship with the body size (i.e., body and tibia length) of a sample of 20 randomly picked parasitoids.

Because we were unable to see eggs inside the logs we considered as successful those attacks on hosts in which the parasitoid spent more than 2 min with its ovipositor inside the host drill (see Spradbery, 1970a, b; Fernández-Arhex & Corley, 2005). The control trial consisted of exposing a single parasitoid on logs of the same hole densities as in the 2-parasitoid test.

To test for the effects of patch richness (i.e., host density), we exposed females to logs offering 0, 2, 4 or 6 oviposition holes. Each treatment was replicated 12 times, in each case using fresh parasitoids and logs.

Data analyses

The parasitoid attack rate was estimated based on the percentage of hosts attacked per unit of patch residence time, modified from Hassell (1978). To analyze the influence of con-specifics and host densities on attack rates and on the number of attacks, we used a linear model assuming a poisson distribution of residuals. In turn, to analyze the influence of con-specifics and host densities on patch residence time, we used a linear model assuming a gamma distribution of residuals. We tested the effect of removing successive factors and variables by means of analysis of variance (ANOVA). Single factors or variables incorporated into significant interactions were maintained in the minimum adequate model (Crawley, 1993). All data analyses were done using the R free software environment (the R freeware statistical package, R Development Core Team, 2008).

Results

Attack rates

Of the two female *I. leucospoides* released on host patches, one of them never attacked hosts. The at-
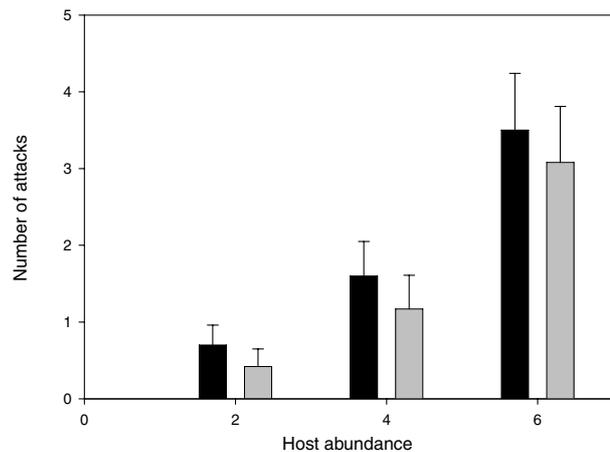
Fig. 1 Number of attacks to hosts by the parasitoid *I. leucospoides* across host densities (means ± SE). Black bars correspond to controls (a parasitoid alone) whereas grey bars are of parasitoids exposed to con-specifics but that have "won" the patch. Patch losers never attacked hosts.

tack rates of those females that remained on the log ('patch winner'), were neither affected by host density ($\chi^2_{(83,1)} = 0.01$, $P = 0.97$) or the presence of con-specifics ($\chi^2_{(82,1)} = 0.009$, $P = 0.96$). However, the total number of attacks was influenced by host availability ($\chi^2_{(83,1)} = 127.96$, $P < 0.00001$) but not by the presence of con-specifics ($\chi^2_{(82,1)} = 126.7$, $P = 0.262$; Fig. 1). There was no interaction between treatment (i.e., parasitoid searching alone, parasitoid with con-specifics) and host density ($\chi^2_{(81,1)} = 0.00998$, $P = 0.99870$).

We also noted that, from a random sample of tested individuals, those that had been 'patch-losers', were significantly smaller than those remaining on the patch (logistic regression: tibia length, $\chi^2_{(1)} = 5.1337$, $P = 0.023$, $n = 20$). "Patch loser" parasitoids may detect competitors through direct encounter (the proportion of trail encounters observed was 30%, 60%, 41% and 100% for 0, 2, 4 and 6 host-density log assays) or else indirectly by, for instance, chemical markers.

Patch residence time

Patch residence time (PRT) of a female *I. leucospoides* was influenced both by host abundance on the patch ($F_{(83,1)} = 15.02$, $P = 0.0002$ and $F_{(83,3)} = 26.69$, $P < 0.0001$ for patch winners and losers, respectively). However, the effect of competition manifested itself only in those parasitoids that left the patch early ($F_{(82,1)} = 2.43$, $P = 0.12$ and $F_{(82,1)} = 4.43$, $P = 0.03$ for patch
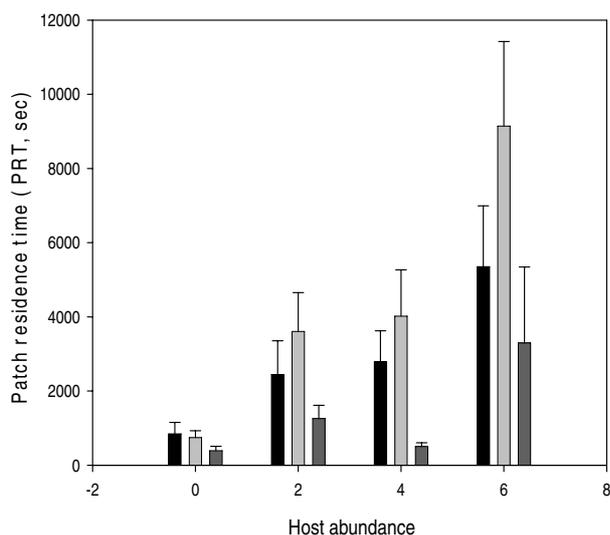
Fig. 2 Patch residence time versus host abundance on a patch, as determined by the number of host drills (means ± SE) of: (A) *I. leucospoides* females which stayed longer on the patch – 'patch winners' (light grey bars), (B) females that left the patch first – 'patch losers' (dark grey bars) and (C) control (black bars).

winners and losers, respectively). There was no interaction between treatment, that is, parasitoid searching alone, parasitoid with con-specifics and host density ($F_{(81,1)} = 2.6840$, $P = 0.105$; Fig. 2).

Discussion

Our results show that con-specific interference during host foraging is important for the parasitoid *I. leucospoides*. While *per capita* attack rates on the patch were constant throughout the assays, the number of hosts attacked was smaller for those parasitoids that always left the log upon direct or indirect encounter with con-specifics. 'Patch losers' also spent less time on logs where con-specifics were present, than when foraging alone on them. However, those individuals that remained on the log after exposure to another female ('patch winners') did not differ in terms of the number of hosts attacked or patch residence time from controls. The females of *I. leucospoides* remaining on the patch were also larger than 'patch losers'.

Our findings imply the display of con-specific competition that is size-dependent. A winning individual, usually the larger of them, undergoes no decrease in the number of attacks or attack rates. Instead 'patch losers', those smaller females that rapidly leave an occupied log upon

detection of the competitor, will not lay any eggs. While no physical combats were observed during our study, avoidance of competition by foraging female parasitoids could be mediated by encounter between individuals or else by chemical cues indicating the presence of another parasitoid. Interference studies in parasitoids have noted that adults react noticeably to other searching individuals nearby. For instance *Venturia cansecens* females exposed to con-specific competition may interrupt host searching for a period, after which one or both foragers disperse from the host area (Waage, 1979; Mills, 1991). Castelo *et al.* (2003) showed that *V. canescens* used chemicals to reduce the cost of interference, as these parasitoids avoid patches with con-specifics. Similar behaviors have been observed when females detect a host which is already parasitized (Rogers & Hassell, 1974) or detect chemical trails left by a previous forager in the same host area (Vinson, 1972). Goubault *et al.* (2005) showed that the proportion of 'retreaters', in *Pachycrepoideus vindemmiae* (Hymenoptera: Pteromalidae) strongly depended on the intensity of competition and on prior experience of competition. Still, the mechanisms behind the behavior displayed by *I. leucospoides* females, especially in those cases where no apparent direct contact was observed, remain unknown.

Patch use rules by foraging parasitoids can also be affected by the presence of other foragers (Godfray, 1994; Pijls *et al.*, 1996; Driessen & Visser, 1997; Visser *et al.*, 1990; Hassell, 2000; Batchelor *et al.*, 2005; Humphries *et al.*, 2006; Goubault *et al.*, 2007). For example, in *Apoanagyrus diversicornis* (Hymenoptera: Encyrtidae) patch residence time was shown to increase with the number of competitors (Pijls *et al.*, 1996). However, our experiments show that for *I. leucospoides*, patch residence time decreased with the presence of another individual. While for one of the two parasitoids tracked in the present study, patches were abandoned early, the other forager remained on the patch a similar time as that displayed by the controls. In this sense, life-time attack rates of patch losers would be adversely affected by con-specific competition.

I. leucospoides may detect competitors through direct encounter as commonly occurred on those logs where host densities were higher (higher on the patch time increases the chance of parasitoid encounter) but was not a necessary condition. Recent Y-tube olfactometer assays have shown that females are attracted to odor sources containing both host semio-chemicals and con-specifics (Fernández-Arhex, 2005). Aggregation by this parasitoid to host-rich logs has also been shown in large arena experiments. These findings have been interpreted as a means of increasing encounters with their hosts, especially when these are found at low densities (Bettinelli,

2001; Fernández-Arhex, 2005). Together, strong aggregation of *I. leucospoides* in the field, and our current findings could imply a behavior aimed at maximizing host-finding, while minimizing the loss of *per capita* profitability. In the field, the host *S. noctilio* attacks several pine trees in close clumps and these clumps are rare, at least during long-standing endemic population phases (Corley *et al.*, 2007). Thus, while con-specific presence can indicate the existence of appropriate hosts, any given attacked tree is likely to be surrounded by several others, probably still free from parasitoid attacks. However, considering study logs as patches may not reflect the behavior displayed by *I. leucospoides* in the field, this aspect requires further study.

Most past interference studies in parasitoids have been carried out in the laboratory in experiments in which parasitoid density was varied but host density was kept fixed (see Kidds & Jervis, 1996; Hassell, 2000). It is also known that for interference results to be of value, parasitoid densities used and host spatial distribution patterns must reflect those found in the field (Free *et al.*, 1977). Another factor to be considered in these kinds of experiments is the size of the experimental arena (Jones & Hassell, 1988). Our study confirms that patch quality is central to patch residence time and the number of attacks. In turn, the territorial behavior displayed is observed for patches bearing different host densities. It remains to be seen how such patterns are affected when more than two parasitoids forage together on the same logs.

Acknowledgments

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