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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

The effect of direct interspecific competition on patch exploitation strategies in parasitoid wasps

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Abstract The presence of competitors may affect the pay-off of individuals' foraging strategies. They should therefore modify their resource exploitation decisions accordingly. In such a direct competition situation, theory predicts that individuals should stay longer on a resource patch than when foraging alone. However, models predicting patch residence time focus on intraspecific competition without agonistic interactions. Here, we investigate the patch use strategies of females of two parasitoid species, *Eupelmus vuilleti* and *Dinarmus basalis*, attacking the same host, *Callosobruchus maculatus,* knowing that *D. basalis* is more aggressive and can exclude *E. vuilleti* during pairwise contests for single hosts. Our results showed that time allocation and oviposition strategies differed in relation to the species and type of competition (i.e., presence/absence of competitor, simultaneous/sequential female introduction or resident/intruder female). *Eupelmus vuilleti* females tended to wait in the patch surroundings for *D. basalis* females' departure to return and exploit hosts parasitized by the opponent (after destruction of her eggs). In contrast, *D. basalis* females tended to self-superparasitize and stay motionless near the hosts. After detecting an *E. vuilleti* female entering the patch, they attacked and chased her permanently from the patch. Females of both species spent less time in the patch when faced with a competitor than when alone. This study is the first to test the influence of direct interspecific competition and arrival order on patch exploitation strategies in parasitoid species, and highlights the necessity to include agonistic behaviors in theoretical models predicting optimal patch residence time in competitive situations.

Keywords Direct mutual interference · Patch time allocation · Oviposition behavior · *Eupelmus vuilleti* · *Dinarmus basalis*

Introduction

When resources of various qualities are patchily distributed in the environment, foragers have to decide which resource to exploit preferentially and when to leave a patch and search for a new one (Charnov 1976; Hassell and Southwood 1978; Wajnberg 2006). The initial model developed to predict foragers' optimal patch residence time, the Marginal Value Theorem (MVT; Charnov 1976), indicates that single foragers adjust their patch time allocation according to the patch quality and the travel time between patches. However, it is not rare that several individuals exploit a patch simultaneously (e.g., Yamamura and Tsuji 1987; Godfray 1994), as other individuals exploiting similar resources (e.g., conspecific or interspecific competitors) are likely to search for and exploit the same patch.

In the presence of competitors, individuals' optimal patch exploitation strategy may differ from that of single foragers, as the pay-off of their foraging decisions is likely to depend on those taken by others (Maynard Smith 1974). Foragers can also interfere directly via agonistic interactions interrupting resource exploitation and therefore

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prolonging its duration (Field and Calbert 1998; Haccou et al. 2003; Hamelin et al. 2007a, b). Hence, foragers will benefit from the departure of their competitors: remaining individuals will continue exploiting the patch and increase their pay-off, in contrast to individuals that left the patch early (Haccou et al. 2003; Hamelin et al. 2007a, b). In parasitoids, early-leaving females can even lose offspring due to the continuing patch exploitation of the remaining females, as females staying in the patch can attack hosts previously exploited by other females (i.e., superparasitism), reducing the probability of the latter obtaining offspring from them (Haccou et al. 2003; Hamelin et al. 2007a, b). Females might therefore engage in a "generalized war of attrition", trying to stay longer on the patch than their competitors (Haccou et al. 2003; Hamelin et al. 2007a, b). Resulting patch residence times should thus increase. Furthermore, the fact that foragers may enter the patch at different times can generate "resource value asymmetries" between them (Maynard Smith and Parker 1976; Hammerstein 1981; Haccou et al. 2003; Hamelin et al. 2007a, b): first-arriving females have parasitized more hosts in the patch than later-arriving females when superparasitism starts. The expected pay-offs for the two types of female are therefore different and should affect their respective optimal patch residence time. The "asymmetric generalized war of attrition" model predicts that foragers arriving early on a patch should stay longer than those arriving later (Haccou and Glaizot 2002; Haccou et al. 2003; Hamelin et al. 2007b; Haccou and van Alphen 2008; Le Lann et al. 2010).

In contrast to these theoretical predictions, the presence of aggressive competitors in some species appears to increase the foragers' patch-leaving tendency (e.g., Wajnberg et al. 2004; Goubault et al. 2005; Fernandez-Arhex and Corley 2010; de Jong et al. 2011). In some cases, females tend to retreat before the start of patch depletion (Goubault et al. 2005), or after contacts and fights with a competitor (Wajnberg et al. 2004). This can then lead to the rapid establishment of a regular distribution of foragers over the different patches available in the environment (de Jong et al. 2011). Additional factors that usually affect optimal patch use by solitary foragers, such as previous experience or physiological state, can also affect individuals' foraging strategies under competition (Goubault et al. 2005; Outreman et al. 2005). For instance, the forager's physiological state, such as a low egg load, can cause a delayed departure from the patch (Field 1998).

Most theoretical and empirical studies have examined patch use strategies in the context of intraspecific competition; the few that have addressed interspecific competition situations focused on indirect competition (Bernstein 1975; Vet et al. 1984; McBrien and Mackauer 1990; Janssen et al. 1995; Takasu et al. 1998; Tamò et al. 2006; Le Lann et al. 2008). To date, we are aware of no study that has explored the effect of the presence of interspecific foragers on individuals' patch exploitation strategies in fighting species. The aim of the present study was therefore to investigate the patch use strategies of females of two parasitoid species attacking the same host in a situation where one species is known to be more aggressive and able to exclude the other during dyadic contests for single hosts (Mohamad et al. 2011).

Eupelmus vuilleti Crawford (Hymenoptera: Eupelmidae) and *Dinarmus basalis* Rondani (Hymenoptera: Pteromalidae) are two sympatric parasitoid species attacking the same host, namely the pupae of *Callosobruchus maculatus,* a bruchid developing in cowpea seeds. The two parasitoid species are known to present different host exploitation strategies under indirect interspecific competition. When confronted with already parasitized hosts, *D. basalis* females tend to avoid parasitizing them as their offspring show low survival chances during larval competition with *E. vuilleti*. In contrast, *E. vuilleti* females tend to prefer hosts parasitized by *D. basalis* to healthy hosts (van Alebeek 1991; Monge et al. 1995; Jaloux 2004). In such cases, they may destroy the egg already present (i.e., commit ovicide) and lay their own clutch (Leveque et al. 1993; Gauthier et al. 1999). Under direct competition for single hosts, however, agonistic interactions between females of the two species are observed, *D. basalis* females being more aggressive. They win most conflicts, preventing *E. vuilleti* females from accessing and exploiting the hosts (Mohamad et al. 2011).

We explored the strategies used by *E. vuilleti* and *D. basalis* when exploiting a patch of hosts simultaneously or sequentially. We expected that *E. vuilleti* females would avoid agonistic interactions with *D. basalis* females, wait for their departure from the patch, and subsequently multiparasitize the hosts. In contrast, we expected that *D. basalis* females would face a trade-off between defending the already parasitized hosts and exploiting the remaining healthy hosts. As the arrival order on the patch may affect the pay-off of patch use strategy for both species, we also tested the effect of simultaneous versus sequential arrivals on female oviposition behaviors and patch residence time.

Materials and methods

Ethics statement

No animal ethics approval was required for this study. We nevertheless handled our insects as gently as possible.

Insect biology and rearing procedures

Eupelmus vuilleti and *Dinarmus basalis* are solitary synovigenic (i.e., females mature eggs throughout their adult life) ectoparasitoid species. They exploit the same hosts

Table 1 Description of the focal females' behaviors that were recorded

Name	Description
Host exploitation	The host was either healthy, already parasitized by the focal or the opponent female
Rejection	The female rejected the host after antennal examination of the seed containing the host or internal examination with the ovipositor
Oviposition	The female laid an egg
Ovicide	The female pierced a previously laid egg with her ovipositor
Host feeding	The female fed from the host hemolymph
Agonistic behavior	
Detection	The female turned her antennae towards the opponent, which eventually retreated
Attack	The female chased her opponent out of the seed and hit her with her antennae or head
Retreat	The female fled upon being attacked

and both feed and lay eggs on them (Huignard 1996; Rivero and Casas 1999). Individuals of both species were collected in crop fields in Togo in 2007. They were then reared separately on larvae and pupae of *C. maculatus* in the laboratory (IRBI, University of Tours, France). Parasitoids and *C. maculatus* were bred according to the methodology described in Jaloux (2004), in a climate room at 33 °C, 70 % relative humidity, and 13:11 h L:D.

Experimental procedures

Females used in the experiments were isolated upon emergence to prevent any previous experience of competition with other females. They were individually placed in Petri dishes (diameter 8.5 cm, height 2.7 cm) for 4 days preceding the experiment. They were provided with water, 1 or 2 males for mating, and 4 cowpea seeds, each infested by a single healthy host (either a fourth instar larva or a prepupa of *C. maculatus*) for oogenesis stimulation and oviposition (Terrasse and Rojas-Rousse 1986). Females were deprived of hosts for 2 h before the test. To study the effect of the presence of an interspecific competitor on patch exploitation strategies in *E. vuilleti* and *D. basalis*, we first studied the behaviors of isolated females of both species foraging on a patch of 4 cowpea seeds, each containing one healthy host ($n = 16$ for each species). We then studied the behaviors of females confronted with a competitor of the other species. For this, one female of each species was introduced on the same host patch, either simultaneously ($n = 27$, with *E. vuilleti* being the focal female in 12 cases) or sequentially (n = 58). In the latter case, the second female was introduced just after the first had parasitized one host. The *E. vuilleti* female was the resident in 29 of the replicates and the intruder in 29 other replicates. In each situation, *D. basalis* was the focal female in half the replicates and *E. vuilleti* in the other half.

The 'patch' was divided into two areas: the central part, containing the hosts, surrounded by a 'waiting area' free of hosts. The central part consisted of a circular area (a 2-cm-diameter circle was drawn under the box to mark this area) containing the infested seeds. The surrounding 'waiting area' consisted of a ring, free of hosts (7 cm in diameter, centered on the central part). Pilot studies showed that females leaving the central part could stay motionless in the waiting area for some time before returning to the hosts, whereas those leaving the waiting area never returned to the patch. In order to catch the females leaving the patch definitively, the patch (i.e., the central part plus the surrounding waiting area) was placed inside a large see-through Plexiglas container (23.5 × 17.5 × 9.5 cm). A video-camera was installed above the container in order to record the behavior of both the focal female and its opponent.

Experiments started with the introduction of the first female and stopped either with the departure of the focal female or after 4 h of observations (preliminary studies showed that 90 % of the females left the patch within 4 h). During the experiments, we recorded all foraging and agonistic behaviors displayed by focal females using The Observer® XT (v.9; Noldus Information Technology, Wageningen, The Netherlands). Table 1 presents these behaviors. Additionally, we noted the number of times focal females entered the waiting area, as well as the time they spent in that zone (hereafter called the 'waiting duration'), the time they spent motionless in the central part of the patch (hereafter called the 'stationary period'), and the total time spent in the whole patch (i.e., overall patch residence time). For the opponent females, we only noted the time spent in the central area of the patch or in the waiting area (i.e., waiting duration) and the number of successful ovipositions. Immediately after the experiments, females were dissected to count the number of mature eggs (egg load), and the cowpea seeds were opened to confirm oviposition by the presence of eggs on hosts. This allowed us to calculate females' initial egg load.

Data analysis

To investigate the effects of (1) the type of competition (i.e., presence or absence of an interspecific competitor, type of arrival on the patch, either simultaneous or sequential, and ownership status, either resident or intruder), and (2) the species the focal female belonged to, and the interaction between these two main effects on the number of ovipositions on the different types of host (healthy, self-parasitized or parasitized by the interspecific competitor), we used log-linear models carried out with GenStat (v.10.1; VSN International, Hemel Hempstead, UK).

The effects of the type of competition, the focal female's species, and the interaction between these two main effects on (1) host handling time, (2) the duration of the stationary period, and (3) the cumulated waiting duration, were quantified by means of Cox regression models (Cox 1972; Collett 1994). The host handling time was computed as the time used by females to exploit the hosts, including the time required to assess the hosts, drill the seeds, lay the egg, commit ovicide, host-feed, and walk from one host to another. It was calculated as the total patch residence time: (stationary duration + waiting duration). We noted that all agonistic behaviors were extremely brief. Their duration was therefore negligible and not taken into account.

The patch residence time and patch-leaving mechanisms adopted by the focal females were also analyzed using Cox's proportional hazards model (Cox 1972; Collett 1994). This model is formulated in terms of hazard rate. Here, this represents the probability per unit of time that a parasitoid female will leave the visited patch, given that she is still on it. In this case, the model assumes that the patch-leaving tendency is the product of a basic tendency to leave the patch (i.e., baseline hazard) and a factor representing the joint effect of all the explanatory variables taken into account (i.e., the covariates). For the focal female, the number of successful ovipositions, host rejections (after host examination by the antennae or the ovipositor), feeding on a healthy host or on a host attacked previously by either the same female or the opponent, and ovicide before an oviposition were used as time-dependent covariates in order to understand their influence on the focal females' patch-leaving tendency. Female species, competition type (i.e., presence/absence of competitor, simultaneous/sequential introduction of females, or resident/intruder female) and egg load of the focal female were considered as fixed covariates. Additionally, we included as time-dependent covariates the number of attacks, retreats and passive contacts (i.e., detection of the presence of a competitor) by the focal females. Finally, the total duration of the stationary period, the total waiting duration, and the total number of visits to the waiting area were also considered as time-dependent covariates. For the opponent females, the covariates tested in the model were their egg load (fixed), the number of successful ovipositions, and the total time spent in the patch and in the waiting area (time-dependent). Table 2 gives a detailed list of all the covariates tested. Their significant effects were assessed using standard likelihood ratio tests with an iterative procedure leading to the most parsimonious model (Collett 1994; Wajnberg et al. 1999). All computations for fitting Cox regression models to the data were done using Splus (Venables and Ripley 1994).

Table 2 List of the explanatory covariates used in Cox's proportional hazards model to identify the patch-leaving mechanisms adopted by the focal females

No.	Covariates
1	Species of the focal female
2	Competition type (treatment code)
3	Focal female's egg load
4	Opponent female's egg load
5	Number of ovipositions in a healthy host
6	Number of ovipositions in a host previously parasitized by the same female
7	Number of ovipositions in a host previously parasitized by the opponent
8	Number of antennal rejections of a healthy host
9	Number of antennal rejections of a host previously parasitized by the same female
10	Number of antennal rejections of a host previously parasitized by the opponent
11	Number of internal rejections of a healthy host
12	Number of internal rejections of a host previously parasitized by the same female
13	Number of internal rejections of a host previously parasitized by the opponent
14	Number of feeding events from a healthy host
15	Number of feeding events from a host previously parasitized by the same female
16	Number of feeding events from a host previously parasitized by the opponent
17	Number of ovicides of focal female's eggs
18	Number of ovicides of the opponent female's eggs
19	Number of visits of the waiting area
20	Overall time spent motionless by the focal female
21	Overall time spent in the waiting area by the focal female
22	Number of attacks
23	Number of retreats
24	Number of passive contacts
25	Number of opponent female's ovipositions
26	Overall time spent in the central part of the patch by the opponent female
27	Overall time spent in the waiting area by the opponent female

Covariates *5–21* concerned the focal female only, and covariates *25–27* the opponent female, whereas covariates *22–24* concerned the behavioral interactions between the two females. Covariates *1–4* were fixed. All others were time-dependent

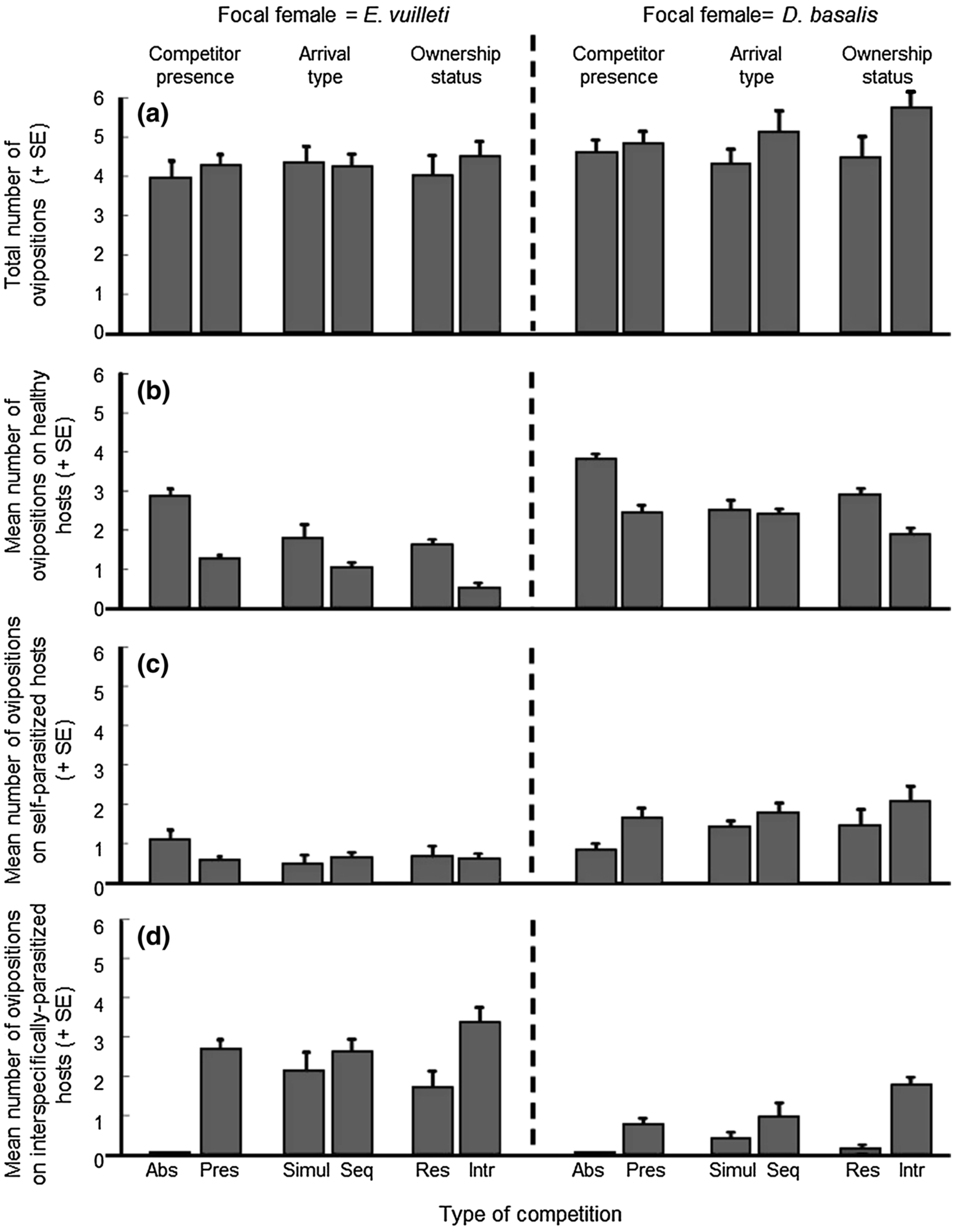

Fig. 1 **a** Total number of ovipositions and oviposition allocation according to host quality, **b** healthy, **c** self-parasitized, or **d** parasitized by the interspecific female, in *E. vuilleti* and *D. basalis* females. Data are presented according to the type of competition: in the absence (*Abs*) or presence (*Pres*) of an interspecific competitor. In the competitive situation, the two females were introduced either simultaneously (*Simul*) or sequentially (*Seq*). In the latter case, the focal female was either the resident (*Res*) or the intruder (*Intr*)

Results

Oviposition strategy

Although the total number of ovipositions made by females of the two species was similar in a competitive situation and when they exploited the patch alone (Fig. 1a; Table 3), the type of host preferentially attacked by the two species differed. When alone, females of both species preferentially laid on healthy hosts (Fig. 1b; Table 3), whereas in a situation of interspecific competition, *D. basalis* females preferred the hosts they had already exploited (self-superparasitism, Fig. 1c; Table 3), and *E. vuilleti* females preferentially attacked hosts previously parasitized by the interspecific competitor (Fig. 1d; Table 3).

Again, regardless of the type of competition (simultaneous versus. sequential arrivals) and their ownership status (resident versus. intruders), females of both species laid as many times in total (Fig. 1a; Table 3), but they allocated their eggs differently to the different types of host. When females were introduced sequentially, females of both species were more likely to lay on healthy hosts when they were residents (Fig. 1b; Table 3) and on hosts parasitized by the interspecific competitor when they were intruders (Fig. 1d; Table 3).

Table 3 Statistical results showing the effect of (*1*) the type of competition (absence versus. presence of an interspecific competitor, simultaneous versus. sequential arrivals, resident versus. intruder females), (*2*) the species of the focal female, and (*3*) the interaction between these two main effects on the number of ovipositions of females according to host quality (healthy, self-parasitized or parasitized by the interspecific competitor)

	Total number of ovipositions	Healthy host	Self-parasitized host	Interspecifically parasitized host
Absence versus. presence				
Type of competition (1)	$F_{1,113} = 0.49$ NS	$F_{1,113} = 41.56$***	$F_{1,113} = 0.63$ NS	–
Species (2)	$F_{1,113} = 3.32$ NS	$F_{1,113} = 33.45$***	$F_{1,113} = 11.13$***	–
Interaction (1) × (2)	$F_{1,113} = 0.04$ NS	$F_{1,\,113} = 4.71$*	$F_{1,113} = 7.37$**	–
Simultaneous versus. sequential arrivals				
Type of competition (1)	$F_{1,81} = 0.87$ NS	$F_{1,81} = 3.32$ NS	$F_{1,81} = 0.66$ NS	$F_{1,80} = 2.76$ NS
Species (2)	$F_{1,81} = 2.07$ NS	$F_{1,81} = 28.81$***	$F_{1,81} = 18.64$***	$F_{1,80} = 25.22$***
Interaction (1) × (2)	$F_{1,81} = 0.81$ NS	$F_{1,81} = 2.89$ NS	$\mathrm{F}_{1,81} = 0.03$ NS	$F_{1,80} = 1.43$ NS
Resident versus. intruder				
Type of competition (1)	$F_{1,54} = 2.87$ NS	$F_{1,54} = 26.04$***	$F_{1,54} = 0.80$ NS	$F_{1,54} = 26.90$***
Species (2)	$F_{1,54} = 2.71$ NS	$F_{1,54} = 43.79$***	$F_{1,54} = 12.50$***	$F_{1,54} = 25.94$***
Interaction (1) × (2)	$F_{1,54} = 0.42$ NS	$F_{1,54} = 7.22$**	$F_{1,54} = 0.51$ NS	$F_{1,54} = 12.81$***

NS $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4 Statistical results showing the effect of (*1*) the type of competition (absence versus. presence of an interspecific competitor, simultaneous versus. sequential arrivals, resident versus. intruder females), (*2*) the species of the focal female (*E. vuilleti* or *D. basalis*), and (*3*) the interaction between these two main effects on total host handling time, stationary period (i.e., total time spent motionless near the hosts) and waiting duration (i.e., total time spent in the waiting zone)

	Host handling time	Stationary period	Waiting duration
Absence versus. presence			
Type of competition (1)	$\chi^2_1 = 1.03$ NS	$\chi^2_1 = 0.02$ NS	$\chi^2_1 = 28.75$***
Species (2)	$\chi^2_1 = 26.4$***	$\chi^2_1 = 24.86$***	$\chi^2_1 = 26.53$***
Interaction (1) × (2)	$\chi^2_1 = 1.92$ NS	$\chi^2_1 = 5.19$*	$\chi^2_1 = 11.88$***
Simultaneous versus. sequential			
Type of competition (1)	$\chi^2_1 = 2.03$ NS	$\chi^2_1 = 0.00$ NS	$\chi^2_1 = 3.77$ NS
Species (2)	$\chi^2_1 = 14.99$***	$\chi^2_1 = 9.25$**	$\chi^2_1 = 3.81$*
Interaction (1) × (2)	$\chi^2_1 = 0.21$ NS	$\chi^2_1 = 0.35$ NS	$\chi^2_1 = 0.35$ NS
Resident versus. intruder			
Type of competition (1)	$\chi^2_1 = 1.73$ NS	$\chi^2_1 = 0.00$ NS	$\chi^2_1 = 1.68$ NS
Species (2)	$\chi^2_1 = 17.67$***	$\chi^2_1 = 6.79$**	$\chi^2_1 = 3.37$ NS
Interaction (1) × (2)	$\chi^2_1 = 1.49$ NS	$\chi^2_1 = 0.77$ NS	$\chi^2_1 = 8.64$**

NS $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Time allocation within the patch

When in the patch, the time that females allocated to handling the hosts or remaining motionless in the central part of the patch (stationary duration) or in the waiting area (waiting duration) strongly differed between species (Table 4). Regardless of the situation, host exploitation took longer in *E. vuilleti* than in *D. basalis* (Fig. 2a; Table 4). When not handling the hosts, the remaining *E. vuilleti* females waited in the surroundings of the patch (i.e., waiting zone) for a longer time than *D. basalis*, especially when *E. vuilleti* was the intruder (Fig. 2c; Table 4). In contrast, in the presence of a competitor, *D. basalis* females stayed motionless near the hosts for extended periods of time (40 min on average), a behavior that was never observed in *E. vuilleti* (Fig. 2b; Table 4). Overall, *E. vuilleti* females tended to stay on average half an hour longer in the patch than *D. basalis* females. This difference was close to significance (patch residence time in *E. vuilleti* females: 178 ± 9 min (mean ± SE); in *D. basalis*: 151 ± 9 min; $\chi^2 = 3.76$; $df = 1$, $P = 0.0525$). However, in both species, the presence of an interspecific competitor did not significantly increase their patch residence time ($\chi^2 = 0.00$; $df = 1$, $P = 1.00$).

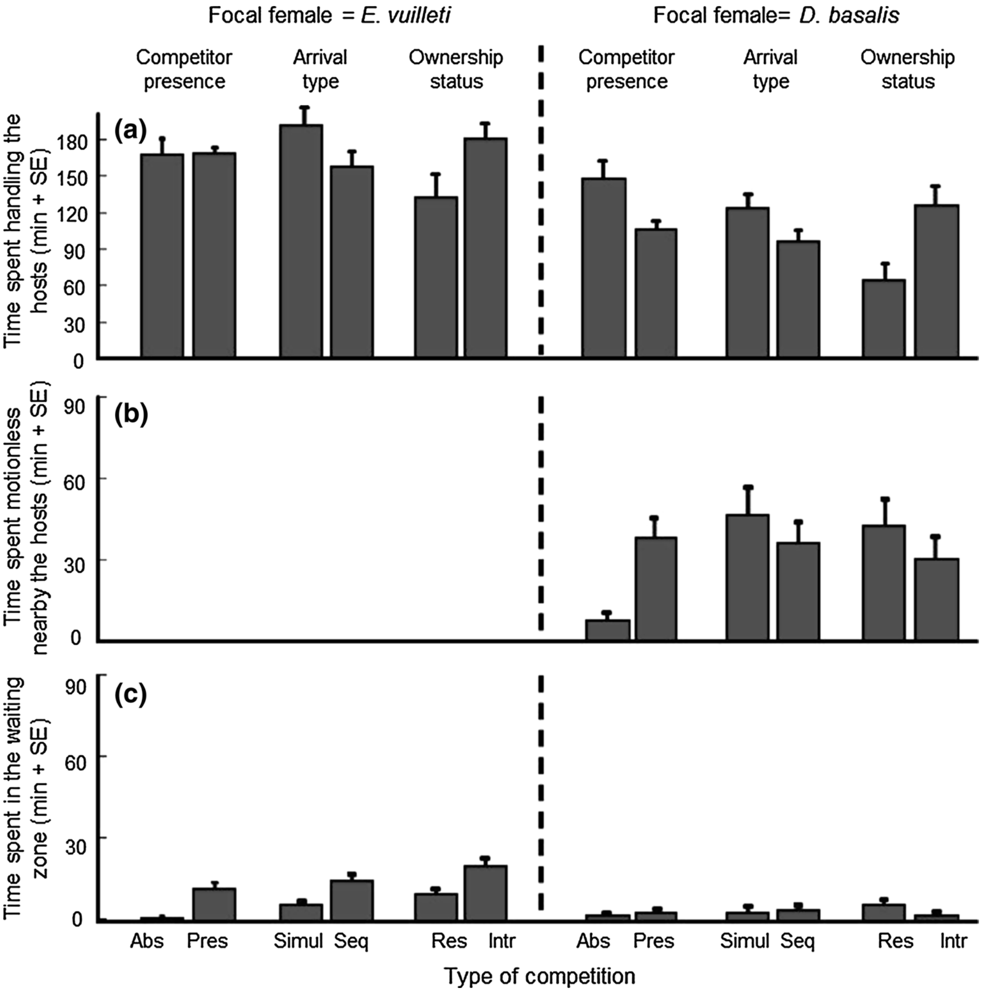

Fig. 2 Time allocation of *E. vuilleti* and *D. basalis* females in the patch: females were either **a** handling the hosts, **b** motionless near the hosts, given that this behavior was not found in *E. vuilleti*, or **c** in the waiting zone. Data are presented according to the type of competition: in the absence (*Abs*) or presence (*Pres*) of an interspecific competitor. In the competitive situation, the two females were introduced either simultaneously (*Simul*) or sequentially (*Seq*). In the latter case, the focal female was either the resident (*Res*) or the intruder (*Intr*)

The patch-leaving rules used by focal females of the two species were identified by means of a Cox's proportional hazards model, and Table 5 gives the estimated effects of all covariates having a significant influence on the *E. vuilleti* and *D. basalis* females' patch-leaving tendencies. In *E. vuilleti*, female egg load had a significant incremental effect on female patch residence time: the larger their egg load, the longer they stayed on the patch. In contrast, as females exploited the patch and laid eggs, their tendency to leave increased: parasitizing a healthy host significantly increased their patch-leaving tendency by a factor of 2.004. Exploiting an already parasitized host had an even stronger effect, increasing their patch-leaving tendency by a factor of 5.089 when the host was already parasitized by the focal female and by a factor of 3.021 when it was parasitized by the interspecific competitor. Rejecting a host already parasitized by the focal female after antennal examination and feeding from healthy hosts also significantly increased their tendency to leave. In contrast, when females committed ovicide of one of their eggs before ovipositing, they significantly increased their patch residence time. A similar effect, almost significant, was observed when the killed egg had been laid by the interspecific competitor. Finally, agonistic interactions between the two females significantly influenced the females' decision to leave the patch: attacking the opponent significantly decreased their tendency to leave by a factor of 0.744, while retreating (i.e., being attacked) significantly increased this tendency by a factor of 1.182.

The patch-leaving tendency of *D. basalis* females was influenced by their egg load and that of their opponent: the greater the number of mature eggs the focal or the competitor females had in their ovaries, the longer *D. basalis* females remained on the host patch. The type of competition also affected their patch residence time. The tendency of *D. basalis* females to leave the patch was 4.376 times greater when they were introduced after *E. vuilleti* females on the patch (i.e., as intruders) than when they were introduced first (i.e., as residents). In contrast, when exploiting a patch alone or arriving simultaneously with *E. vuilleti* females on the patch, their patch-leaving tendency was less than when they were residents. *D. basalis* patch residence

Table 5 Estimated regression coefficients (β), standard errors of β (*SE*) and hazard ratios (*exp* β) for the covariates having a significant effect ($P < 0.05$) on the patch-leaving tendency of focal females only

Species and covariates	β	SE	exp β	χ^2 (*df*)	*P* value
Eupelmus vuilleti					
Focal female's egg load	−1.314	0.241	0.268	41.984 (1)	<0.001
Oviposition on a healthy host	0.695	0.281	2.004	5.959 (1)	0.01
Oviposition on a self-parasitized host	1.627	0.388	5.089	17.990 (1)	<0.001
Oviposition on an inter-specifically parasitized host	1.106	0.268	3.021	17.313 (1)	<0.001
Antennal rejection of a self-parasitized host	0.679	0.1220	1.972	34.563 (1)	<0.001
Ovicide of own egg	−7.737	19.778	0.000	6.039 (1)	0.013
Ovicide of an opponent's egg	−0.679	0.380	0.506	3.414 (1)	0.06[a]
Feeding from a healthy host	1.150	0.453	3.158	6.446 (1)	0.011
Attack	−0.295	0.107	0.744	7.964 (1)	<0.01
Retreat	0.168	0.050	1.182	11.201 (1)	<0.001
Dinarmus basalis					
Focal female's egg load	−0.623	0.135	0.536	27.278 (1)	<0.001
Opponent's egg load	−0.611	0.215	0.543	9.429 (1)	<0.01
Type of competition: 'absence'	−4.537	1.313	0.010	19.016 (3)	<0.001
Type of competition: 'arriving-together'	−0.180	0.771	0.835		
Type of competition: 'Db-intruder'	1.476	0.805	4.376		
Type of competition: 'Ev-intruder'	0.000	–	1.000		
Oviposition on a healthy host	1.733	0.480	5.658	16.717 (1)	<0.001
Opponent female's ovipositions	1.093	0.317	2.984	12.594 (1)	<0.001
Antennal rejection of a healthy host	0.503	0.162	1.653	8.004 (1)	<0.01
Internal rejection of a healthy host	3.370	0.770	29.067	15.070 (1)	<0.001
Time spent in the waiting area by the focal female	2.768	0.326	15.928	166.546 (1)	<0.001

χ^2 corresponds to likelihood ratio tests

[a] We have retained this value because it is marginally significant

time was also influenced by its host exploitation behavior: parasitizing or rejecting a healthy host, after either external or internal examination, had a significant decremental effect on the time females spent on the patch. Similarly, the number of ovipositions performed by the opponent female had a significant decremental influence. Visiting the waiting area also increased the tendency of females to leave the patch. In contrast to *E. vuilleti*, we observed no significant effect of agonistic interactions with the opponent on the patch residence time of *D. basalis*.

Discussion

We studied the effect of direct interspecific competition on the patch exploitation strategies of foragers in two parasitoid species, *E. vuilleti* and *D. basalis,* competing for the same patch of hosts. Both species showed agonistic behaviors but they presented different foraging strategies. We discuss below the advantages of these strategies in such a competitive situation.

Oviposition decision and time allocation

In situations of direct interspecific competition, *E. vuilleti* females were frequently attacked by *D. basalis* females. Instead of inciting them to leave the patch, *E. vuilleti* females waited on average 12 min motionless in the surroundings of the hosts (i.e., in the 'waiting zone') until their opponents' departure. They then walked back to the hosts and multiparasitized them. This 'waiting strategy', already reported in *E. vuilleti* during dyadic intraspecific contests for single hosts (Mohamad et al. 2012), also seems advantageous for this species in interspecific competition. Indeed, when exploiting an already parasitized host, 93 % of *E. vuilleti* females found and re-used the hole drilled by the *D. basalis* female through the seed. Accessing the host by reusing this orifice is 6 times faster than drilling a new hole and would prevent the risk of damaging their ovipositor, which is long and flexible (Terrasse and Rojas-Rousse 1986; van Alebeek 1991; Jaloux 2004). It may also increase the probability of locating the opponent's egg and successfully committing ovicide, as observed in *P. vindemmiae* (Goubault et al. 2004). Additionally, in multiparasitized hosts, the survival probability of *E. vuilleti* offspring is high: their larvae have a 66 % chance of winning the competition against *D. basalis* offspring when the time interval between the two ovipositions is less than one hour (Gauthier et al. 1996, 1999).

Dinarmus basalis females adopted a different strategy when faced with interspecific competition. They invested in self-superparasitism, laying more than one egg in most hosts. This type of behavior is common in parasitoids experiencing competition: by out-numbering the opponent's offspring, they increase the probability of their offspring winning the larval competition (van Alphen and Visser 1990). In the presence of an *E. vuilleti* female, *D. basalis* wasps also showed a particular behavior: they spent extended periods of time (on average 40 min) motionless near or on the hosts. This stationary behavior was then interrupted, either by the *D. basalis* female resuming the exploitation of the patch or by her detection of the presence of the competitive *E. vuilleti*. In the latter case, the *D. basalis* females quickly attacked and chased away their opponent. By sitting motionless on the patch, females may be less detectable by *E. vuilleti* females, which, as a result, may leave the waiting zone and approach the hosts. As observed in *Trissolcus basalis* (Field 1998), the stationary behavior may therefore allow females to monitor and assess the risk of competition while exploiting the patch. These waiting strategies developed by *E. vuilleti* in the surroundings of the patch and by *D. basalis* near/on the hosts are reminiscent of the 'waiting game' observed during intraspecific contests for host patches in *T. basalis* (Field et al. 1998; Wajnberg et al. 2004). However, in *E. vuilleti* and *D. basalis*, these waiting strategies did not lead to a war of attrition (Maynard Smith 1974), as female patch residence time did not increase in competitive situations compared to when females exploited the patch alone.

Patch-leaving rules under direct interspecific competition

Variations in the female's physiological status, such as egg load, are known to influence the foraging behaviors of parasitoids (Minkenberg et al. 1992). Here, it clearly affected their tendency to leave the patch, females with larger egg loads staying longer on the patch. This could be due to a higher motivation of these females to access a reproductive site (Mohamad et al. 2010), leading them to spend more time exploiting the available hosts and defend the patch for an extended period of time. Moreover, we observed that *D. basalis* females delayed their departure from the patch as their opponent's egg load increased. Although the information they use to assess it remains unknown, it seems particularly advantageous, as the opponent's egg load is likely to reflect its probability of exploiting hosts. Multiparasitism represents a considerable threat for *D. basalis* offspring, which, as previously mentioned, tend to lose larval competitions against *E. vuilleti* (Gauthier et al. 1999).

Females of both species also appeared to use local information about the change in patch quality to determine when they left the patch (as classically observed in single foragers; see Wajnberg 2006, for a review). Overall, oviposition and rejection of healthy and already parasitized hosts increased the tendency to leave the patch. This decremental effect of host exploitation on females' patch residence time seems adapted to the regular distribution of *C. maculatus* in the natural environment (Murdock 1959). Larvae and nymphs of this bruchid beetle are located inside the cowpea seeds, which are grouped within pods. Each oviposition and detection of already parasitized hosts would therefore indicate that fewer healthy hosts remain to be discovered within the pod. The probability of a female leaving such a patch should increase accordingly.

Although females' decisions to leave the patch were influenced by the presence of the interspecific competitor in both species, the information used was different. In *E. vuilleti,* patch-leaving decisions were affected by direct agonistic interactions with the competitor: attacking led females to remain on the patch, whereas being attacked and thus retreating favored their departure. Several types of information might be collected by females during these aggressive encounters. Upon detecting the presence of a competitor, they could assess their relative fighting ability or motivation to access and exploit the hosts. Receiving an attack may inform them that the opponent is more prone to win the contest. In this case, leaving the patch early would therefore be adaptive. In contrast, in *D. basalis*, females' tendency to leave increased with the mere presence of an opponent. The effect was more pronounced when they arrived after the *E. vuilleti* female had started to exploit the patch, indicating that they perceived the time gap between the two females' arrivals. Direct interactions with the interspecific competitor did not significantly affect the patch residence time of *D. basalis* females. The simple detection of the presence of the opponent female was sufficient to affect their decision. Further experiments are needed to identify the cues or signals used by females to perceive the presence of a competitor as well as their order of arrival. In any case, the fact that the females that arrived first stayed longer on the patch than those that arrived second is in line with the predictions of the "asymmetrical war of attrition" model (Haccou and Glaizot 2002). However, this model also predicts that foragers will stay longer than when alone, which was not the case here. It should be noted that the different models developed to predict the patch-leaving rules of foragers experiencing competition (Haccou and Glaizot 2002; Haccou et al. 2003; Hamelin et al. 2007a, b; Haccou and van Alphen 2008) do not assume any direct, costly interactions between them. Here, as observed in other fighting parasitoid species such as *T. basalis* (Wajnberg et al. 2004) and *P. vindemmiae* (Goubault et al. 2005), it seems that agonistic behaviors (or the risk of experiencing them) considerably affect females' patch-leaving decisions and favor shorter residence time.

Conclusion

Here, we observed that the two species adopted different strategies when competing agonistically for host patch exploitation. Females of the more aggressive species, *D. basalis,* tended to invest in host defense and self-superparasitism, while *E. vuilleti* females, which are less aggressive but more efficient at exploiting already parasitized hosts, tried to remain undetected until *D. basalis* left and then looked for multiparasitism opportunities. If they were to be detected and attacked by *D. basalis,* they would instead leave the patch earlier. Models predicting patch residence time in competitive situations have often been tested in parasitoid species, and we could expect to observe similar strategies in interspecific consumers directly competing for a resource that can be re-used or shared. In co-existing species exploiting similar resources, one is often more aggressive and can locally displace the other. We could nevertheless expect the subordinate species to adopt some sort of waiting strategy. This might be the case in the subordinate hermit crab, *Paguristes perrieri*, when foraging in the presence of its sympatric *Clibanarius digueti* competitor: they are more submissive and tend to lose access to the food pellet, but if the pellet is broken, they feed more frequently on broken pieces (Tran et al. 2014).

Finally, contrary to predictions, data from our study show that the presence of an interspecific competitor does not increase foragers' overall patch residence time. Early departure from the patch may be due to the risk and costs associated with agonistic behaviors. We thus urge theorists to include in their models of patch residence time in competitive situations the possible occurrence of energy-demanding aggressive behaviors, which may lead to the injury or even death of one forager (Pérez-Lachaud et al. 2002; Batchelor et al. 2005), as they can strongly impact the patch use strategies of foragers and consequently their distribution in the environment.

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