



Original Article

Let the most motivated win: resource value components affect contest outcome in a parasitoid wasp

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Studying physical contests for indivisible resources is a major theme in behavioral ecology. Intensity (aggressiveness) and outcome of such contests may be influenced by individual abilities to gain and keep the resource (resource-holding potential, RHP), but also by the value they place in the resource (resource value, RV). Contestants can assess resource quality directly (objective RV) or estimate it according to their physiological status and their experience (subjective RV). In some parasitoid species, adult females fight for hosts on which they lay eggs and feed. Here, we studied contests between 2 females of the solitary parasitoid *Eupelmus vuilleti* when exploiting simultaneously a host: a fourth instar larva or a pupa of the cowpea seed beetle *Callosobruchus maculatus*. We first demonstrated that fourth instar larvae represent a resource of higher objective RV because offspring that developed on such hosts were heavier. We then showed that both objective (host quality) and subjective (initial egg load and habitat quality) RV did not influence oviposition decisions, but interacted to affect aggressiveness and contest outcome. Females won more frequently when they had more mature eggs than their opponent, but this effect was less pronounced when fighting for a high-quality host. In addition, females from high-quality habitat were more aggressive and more frequently won contests over low-quality hosts, whereas females from low-quality habitat were more aggressive and more frequently won contests over high-quality hosts. This experiment thus highlights the complex relationships existing between key factors that affect animals' conflict resolution.

Key words: aggressiveness, conflict resolution, *Eupelmus vuilleti*, oviposition decision.

INTRODUCTION

Intraspecific competition for access to indivisible resources is common in the animal kingdom and has therefore received major attention from behavioral ecologists (Maynard Smith and Parker 1976; Kokko 2013). In a wide range of species, pairs of individuals compete via agonistic contest behaviors for food, mates, or territories (Huntingford and Turner 1987; Archer 1988; Hack 1997). Even if most of these physical contests occur between males, they are also observed between females, between juveniles and adults, between parents and offspring, or between and within social groups (Riechert 1998).

Game theory models have identified factors expected to influence the outcome of such dyadic contests (Maynard Smith 1982). A common predictor is the asymmetry that exists between contestants in terms of their ability to gain and hold access to the resource (resource-holding potential, “RHP”; Maynard Smith

1974; Parker 1974). The RHP of an individual usually relates to intrinsic factors such as its body size or mass (Hack 1997; Riechert 1998; Archer and Thanzami 2007), its physiological status, or the size of its weapons (Huntingford and Turner 1987; Andersson and Iwasa 1996). The individual winning the resource is typically the contestant with the higher RHP (Parker 1974; Maynard Smith 1982; Elias et al. 2008; Arnott and Elwood 2009).

Asymmetries in the value of the resource (hereafter “RV”) between contestants play an additional role in influencing fighting intensity and determining contest outcome (Maynard Smith and Parker 1976; Hammerstein 1981; Enquist and Leimar 1987; Arnott and Elwood 2008). Such a phenomenon has been observed in insects (Brown et al. 2007), arthropods (Gherardi 2006), birds (Ewald 1985), amphibians (Verrell 1986), and fishes (Lindström 1992), with the individual having a higher RV generally winning the contest (Parker 1974; Maynard Smith 1982; Kokko 2013). Resource value (RV) can firstly depend on properties intrinsic to the resource (the “objective” RV) which can be detected by contestants and yield a certain fitness benefit if obtained (Gherardi 2006; Goubault et al. 2007a). For example, a piece of food of a large

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size or high-nutritive value represents a resource providing a high fitness advantage (Chancellor and Isbell 2008), and aggressiveness during contests for such a resource may therefore be elevated (Gilley 2001; Stockermans and Hardy 2013). Secondly, differences between contestants in their physiological status and experience of resource availability may also change the value of a given resource, causing individuals to take more risks, fight harder, and spend more energy to acquire or defend it. Thus, subjective RV (Enquist and Leimar 1987) refers to the value that each contestant places on the resource, independent of its objective value. For example, individuals deprived of a particular resource (e.g. mate or food) are predicted to value that resource more highly than if they had recently had access to it. They should fight more, with a higher probability of winning contests (Hurd 2006; Brown et al. 2006, 2007; Dissanayake et al. 2009). In some cases, high RV can help individuals to overcome inferior RHP (Ewald 1985; Verrell 1986; Gherardi 2006).

In parasitoid wasps, larvae depend entirely on the host for their development, as they feed exclusively on its tissue until they emerge as adults. Fitness of individuals therefore strongly depends on the value of the host and, thereby, on the oviposition decisions made by their mother (Godfray 1994; Henry et al. 2005; Todoroki and Numata 2017). In many species, oviposition behavior is size-, age-, or stage-specific (Heinz and Parrella 1989; Walde et al. 1989; Kidd and Jervis 1991; Godfray 1994; Chau and Mackauer 2001; Cebolla et al. 2017). Thus, oviposition is usually directed toward larger, older, or later-stage hosts, as the size of offspring resulting from oviposition on larger hosts is often higher than that from smaller, younger, or earlier-stage hosts (Charnov 1985; Lacoume et al. 2006). Oviposition on low-quality hosts is only predicted to occur when egg load is high or when high-quality hosts are rare (McGregor 1997). Lifetime reproductive success is also maximized by accepting low-quality hosts for oviposition only when the probability of encountering high-quality hosts is low (e.g. see Mangel and Roitberg 1989; Roitberg et al. 1992).

Moreover, hosts represent a limited resource for which female parasitoids can compete to lay their eggs. Because outcome of the competition directly influences their fitness (Petersen and Hardy 1996; Field and Calbert 1999; Batchelor et al. 2005), it is not surprising that physical contests between females for host access have already been observed in some parasitoid species, such as *Venturia canescens* (Hughes et al. 1994), *Trissolcus basalidis* (Field and Calbert 1999), *Eupelmus vuilleti* (Mohamad et al. 2010), *Dinarmus basalidis* (Mohamad et al. 2013), and several bethylids (Petersen and Hardy 1996; Pérez-Lachaud et al. 2002; Goubault et al. 2007a, 2007b). Several factors that modify the RHP and RV of contestants have been shown to influence aggressiveness and conflict resolution. For example, larger females (i.e. with a higher RHP) are more likely to win access to the host (Petersen and Hardy 1996; Goubault et al. 2007a). Regarding objective RV, females defending larger hosts or more vulnerable brood usually have a higher probability of winning (Humphries et al. 2006; Goubault et al. 2007b). The quality of the habitat previously experienced by females can also influence females' subjective host value and therefore contest outcome. For example, females that have experienced a habitat poor in hosts should value hosts more and win contests more often than females that have experienced high host availability (Mohamad et al. 2010). However, the opposite result was observed in *P. vindeminae*, with rich-habitat females being more likely to win host access than poor-habitat females (Goubault et al. 2007a). Authors of this study hypothesized that females from rich habitat had potentially

greater opportunities to acquire energy through host feeding during exploitation of previous patches, resulting in greater host-protection abilities (i.e. higher RHP). Finally, females with more mature eggs present in their ovaries (i.e. with a greater "egg load") win contests more frequently in several species (Stokkebo and Hardy 2000; Mohamad et al. 2010; but see Goubault et al. 2007a). Thus, greater egg load has been hypothesized to enhance the value that females place on the hosts, with females having more mature eggs being more ready to oviposit. Nevertheless, little is known about the influence of both objective and subjective RV on contest outcomes and aggressiveness, and studies have been studied mainly in only 2 gregarious parasitoids, *Goniozus nephantidis* (Humphries et al. 2006) and *Goniozus legneri* (Stockermans and Hardy 2013).

In the present study, we therefore tested the relative effect of both objective and subjective host value on 1) female oviposition decisions and 2) contest outcomes and aggressiveness, using *E. vuilleti* Crawford (Hymenoptera: Eupelmidae). *E. vuilleti* is a solitary (i.e. only one juvenile can develop per host, supernumerary offspring being killed during larval competition) ectoparasitoid. Females parasitize and feed upon larvae and pupae of *Callosobruchus maculatus* (Fab) (Coleoptera: Bruchidae), which infest seeds of *Vigna unguiculata* (L.) Walp (Fabaceae; Terrasse and Rojas-Rousse 1986). In sub-Saharan Africa, cowpea seeds are traditionally stored in granaries where populations of both hosts and parasitoids can reach high densities, leading *E. vuilleti* females to experience intense intraspecific competition. When several females are simultaneously present on a patch, they tend to protect the host that they exploit by displaying agonistic behaviors towards conspecific competitors (Mohamad et al. 2010). Moreover, Terrasse and Rojas-Rousse (1986) have shown that the number of eggs laid by females varied according to the age of hosts; wasps laid fewer eggs on fourth instar (hereafter: "L4") larvae than on pupae. Although this could suggest that later-stage hosts represent higher-quality resource, no work has directly studied the resulting fitness benefits for females.

We designed a first experiment to measure the difference in fitness returns that females obtain when ovipositing on larval and pupal hosts (i.e. the objective RV, measured in terms of offspring survival, developmental time, and body mass at emergence). We expected them to gain higher fitness by laying eggs on later-stage/larger hosts. We further studied the role of females' previous habitat quality on oviposition decisions. In a second experiment, we tested whether aggressiveness and resolution of conflicts between females were affected by the previous habitat quality (i.e. subjective RV) and/or the objective value of the host during contests. We expected that individuals with a low-quality oviposition experience would place a higher value in high-quality hosts and therefore would be more aggressive and would ultimately be more likely to win contests for those hosts.

MATERIAL AND METHODS

Laboratory breeding

We collected *E. vuilleti* on cowpea seeds from crop fields in Togo in 2007. We then bred parasitoids in the laboratory (IRBI, University of Tours, France) on larvae and pupae of *C. maculatus*, according to the methodology described by Jaloux et al. (2004). We carried out all experimental procedures in a climate room at 30 °C and 12:12 h light: dark. We dissected cowpea seeds to collect hosts for *E. vuilleti*, and we then individually placed them in a standard transparent gelatin capsule (length: 2 cm, diameter: 0.6 cm). This system mimics a cowpea seed while not altering the oviposition behavior

of females and allows for easier observation of the number of eggs laid by females (Gauthier and Monge 1999). Previous studies have shown that after a period of adaptation, parasitoid females behave in the same manner in the presence of hosts inside seeds or capsules (Gauthier and Monge 1999; Jaloux et al. 2004), although the number of eggs are slightly lower on hosts inside capsules (Damien et al. 2001). Under such conditions, eggs hatch during the day following oviposition, whereas adults emerge between 20 to 24 days later (Mathiron A, personal observation).

Females used in the following experiments emerged in isolation, preventing them from having any previous experience of oviposition and competition. We individually placed them in petri dishes (diameter: 8.5 cm; height: 2.7 cm), provided with cotton soaked in water for the 3 days preceding the experiments. *E. vuillei* is a synovigenic parasitoid species: emerging females possess a few mature eggs and they mature additional ones throughout their adult life. Thus, if females can lay eggs from the day of their emergence, their oviposition activity increases over time and is maximum 3 days later (Jaloux et al. 2004). To stimulate oogenesis (Terrasse and Rojas-Rousse 1986), we also gave one male to females during the first day.

Experiment 1: effect of objective and subjective RV on oviposition decisions and female fitness

To investigate the influence of objective and subjective RV on female oviposition decisions, we randomly assigned 40 wasps to one of 2 ‘‘oviposition pre-experiences’’: at their emergence, we supplied 20 females with one L4 larva replaced daily and 20 other females with 1 pupa, also replaced daily. When they were 3 days old, we deprived wasps of host for at least 2 h before the start of the experiment so that they were more ready to oviposit. We then individually introduced each female into a new petri dish supplied with 2 types of hosts, 1 L4 larva and 1 pupa in cellulose capsules, for 3 h. We noted the first host that females were in contact with and on which host they oviposited first. We removed females after the end of the experiment. To further determine the fitness benefits provided by both types of hosts, we let the offspring develop after checking that a single egg was present (supernumerary eggs were removed). We then followed the development of each offspring until they emerge as adults: we noted their mortality, development time, and body mass at emergence using an electronic balance (Ohaus Discovery® model, accuracy: 0.01 mg).

Experiment 2: effect of objective and subjective RV on aggressiveness and contests outcome

To investigate the influence of objective and subjective RV on female competitive behaviors, we randomly assigned females at their emergence to 2 different oviposition pre-experiences: we supplied them with either 1 L4 larva or 1 pupa of *C. maculatus*, replaced daily for 3 days. To allow wasp identification during contests, we marked them on the dorsal part of their thorax with a dot of bright-yellow or bright-red acrylic paint. Data showed that paint color did not affect contest outcomes (wasps painted red won 34 of 63 contests; binomial test: $P = 0.61$). As in Experiment 1, we deprived females of hosts for at least 2 h before the start of the experience. At the beginning of the observation, we simultaneously introduced 2 wasps into an apparatus consisting of a plastic block made of 3 chambers linked by a slot (Petersen and Hardy 1996).

We ran all contests between 2 females with different oviposition pre-experiences (i.e. either with L4 larvae or pupae), challenging for

either 1 L4 larva ($n = 29$) or 1 pupa ($n = 34$) located in gelatine capsules and previously placed in the central chamber of the contest arena. Contestants were of the same age (3 days old), marked with different colors and visually matched for size (post-test data analysis confirmed that contestants of a same dyad did not differ significantly in body mass; Student paired-test: $t = 0.57$, $P = 0.57$). Both females could freely move into the entire contest block. Observations lasted 1 h or were stopped when either one of the female exited the central chamber or neither of the females touched the host or displayed any agonistic interactions for at least 2 min.

During all tests, we recorded the oviposition and the agonistic behaviors displayed by each female. Upon detection of a conspecific competitor (females raised their antennae in the direction of their opponent), females frequently interrupted their behavioral oviposition sequence (Mohamad et al. 2010). They can either simply kick their opponent with their legs without taking their ovipositor out of the capsule (defensive behavior) or this can escalate to a full attack, in which case one female generally chases her opponent away from the capsule, hits her with her head, and mounts her. This chasing, hitting, and mounting can lead the loser to leave the central chamber of the arena. We therefore considered only these behaviors, collectively termed as ‘‘attack,’’ in the rest of the study. When both females of a dyad stayed in the central chamber during the whole time of observation, we determined the winning female as the ovipositing one.

We immediately froze wasps at -20 °C after the experiments. We weighed them using an electronic balance (Ohaus Discovery® model, accuracy: 0.01 mg) and we then dissected them to count the number of mature eggs in their abdomen (i.e. egg load). Finally, after each contest, we counted the number of eggs laid on the host by the winning female to determine their egg load before the contests (i.e. initial egg load).

Statistical analysis

We performed data analyses with the software Rstudio (RStudio Team 2016), using $\alpha = 0.05$. Our general approach was to use, when possible, parametric analyses in which the assumed distribution of residuals was matched to the data rather than transforming data to fit standard assumptions (Wilson and Hardy 2002; Briffa et al. 2013). However, we used nonparametric tests when conditions of application were not verified.

Experiment 1

We first checked that initial egg load was not significantly different between females that had previously oviposited on L4 larvae (mean egg load \pm SE: 4.9 ± 0.5) and those that had experienced oviposition on pupae (egg load: 5.2 ± 0.4 ; Student test: $t = -0.54$, $P = 0.59$). We defined female oviposition decisions as a binary response: 0 = the female first oviposited on the larva and 1 = the female first oviposited on the pupa. We then ran a generalized linear model (GLM) assuming a binomial distribution of errors to determine if female oviposition decisions were influenced by initial egg load, oviposition pre-experience, and the type of host first encountered. Moreover, we defined offspring’s status as a binary response: 0 = offspring died before reaching adulthood and 1 = offspring reached adulthood. We tested the development time of progeny on both host types by using a Cox proportional hazards regression model, which allows for censored data. We subsequently performed a generalized linear mixed model (GLMM) with a binomial error distribution to investigate the influence of host type on

offspring mortality during development, fitting mother identity as a random factor. Finally, we used a linear mixed-effects model (LMM) to test the influence of the mother's body mass and the type of host on the body mass of offspring at their emergence, again fitting mother identity as the random factor. As only 2 males emerged in our experiment, we decided to discard these data from the analyses because males usually emerge before females and are smaller (Rojas-Rousse et al. 2005; Mathiron A, personal observation).

Experiment 2

We verified that the initial egg load did not differ between females that had previously oviposited on L4 larvae (mean egg load \pm SE: 4.4 ± 0.4) and those that did on pupae (egg load: 5.3 ± 0.6 ; Mann–Witney test: $U = 1832.5$, $P = 0.45$). The number of attacks were positively correlated between both females of the same contest (Spearman rank correlation test: $r_s = 0.47$, $P < 0.001$). We therefore chose to use relative attack ratios of focal females in our analyses, calculated as the following ratio: “number of attacks of the focal female / total number of attacks during contest (i.e. attacks of the focal female + that of her opponent).” We performed a GLM with a quasi-binomial error distribution to explore the influence of contestants' difference in egg load, oviposition pre-experience and host quality on the relative attacks of focal females. We finally ran a GLM assuming a binomial error distribution to explore the influence of initial egg load difference between contestants (i.e. initial egg load of the focal female minus that of her opponent), oviposition pre-experience, and host quality on contest outcomes. To run this analysis, we randomly assigned one of the 2 females of each replicate as the focal female, using the ALEA function of Microsoft Excel and we defined contest outcome as a binary response: 0 = the focal female lost and 1 = the focal female won.

RESULTS

Experiment 1: effect of objective and subjective RV on oviposition decisions and female fitness

Oviposition decisions

Neither initial egg load and oviposition pre-experience nor their interaction affected female oviposition decisions (Table 1). However, analyses showed that the first host chosen by the female for oviposition was the first host they have encountered (Table 1).

Female fitness

Statistical analyses showed that the type of host on which daughters developed did not affect neither their development time (Cox proportional hazards regression model: Likelihood ratio test = 2.64, $P = 0.10$) nor their mortality during development (GLMM: $\chi^2 = 1.402$, $df = 1$, $P = 0.24$). There was no interactive effect of host type and mother body mass on the body mass of daughters at their emergence. However, their body mass varied with host type: daughters were significantly larger when they developed on a L4 larva than on a pupa (LMM: $\chi^2 = 11.24$, $df = 1$, $P < 0.001$; Figure 1).

Experiment 2: effect of objective and subjective RV on aggressiveness and contest outcome

The relative number of attacks displayed by the focal females was significantly influenced by interaction between pre-experience oviposition and host quality, whereas no other interaction was

Table 1

Effect of females' initial egg load, oviposition pre-experience, and the type of the first encountered host on their oviposition decisions

Factors affecting females' oviposition decisions	df	Estimates	G	P
Intercept		0.033		
Initial egg load	1	-0.42	1.27	0.26
First host (pupa)	1	21.53	44.03	<0.001
Pre-experience (pupae)	1	-21.6	1.17	0.28
Initial egg load \times first host (pupa)	1	0.42	0	1
Initial egg load \times pre-experience (pupae)	1	0.42	0	1
First (pupa) \times pre-experience (pupae)	1	21.6	0	0.99
Initial egg load \times first host (pupa) \times pre-experience (pupae)	1	-0.42	0	1
Residuals	32			
Total	40			

P values of significant explanatory variables are highlighted in bold font.

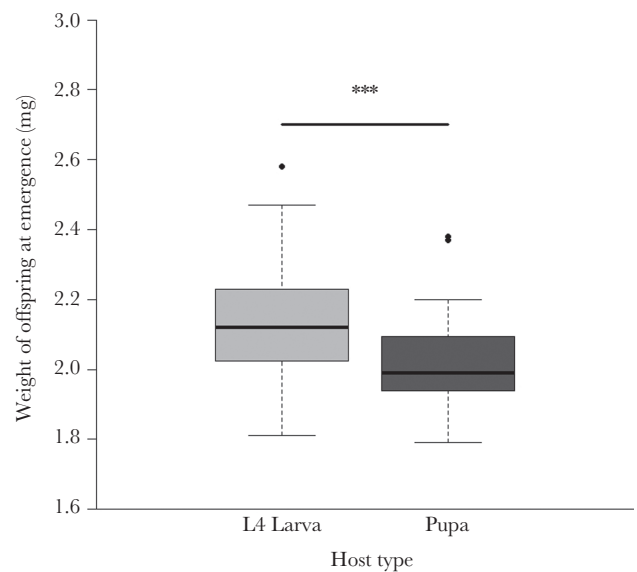


Figure 1

Body mass of *E. vuillei* daughters at their emergence from a L4 larva ($n = 31$) or a pupa ($n = 27$). *** $P < 0.001$.

significant (Table 2). Females with a L4 larvae oviposition pre-experience attacked significantly more when the contested host was a pupa than a L4 larva. In contrast, females with an oviposition pre-experience on pupae attacked significantly more when competing for a L4 larva than a pupa (Figure 2a).

The probability of a focal female winning was significantly influenced by interactions between the difference in initial egg load and host quality and between oviposition pre-experience and host quality, but not by the interaction between the difference in initial egg load and oviposition pre-experiences (Table 3). Females had higher probabilities of winning contests when they had more mature eggs than their opponent, but this effect was less pronounced when the contested host was a L4 larva. Moreover, the probability of a focal female with pupae oviposition pre-experience winning a contest was significantly higher when competing for a L4 larva, whereas females that had previously experienced oviposition on L4 larvae had a higher probability of winning contest for a pupa (Figure 2b).

DISCUSSION

The purpose of our study was to test the relative effect of both objective and subjective host value on female oviposition decisions and conflict resolution in the solitary ectoparasitoid *E. vuilleti*. By measuring the impact of 2 host types on different offspring life history traits (used as a proxy for mothers' fitness), we first showed that *C. maculatus* 4th instar larvae and pupae represent resources with different resulting fitness benefits for *E. vuilleti* mothers, hence differing in objective RV. Moreover, though different components of objective (host type) and subjective (initial egg load and availability in both host types) RV did not influence female oviposition decisions, they interacted to affect female aggressiveness and contest

Table 2

Effect of initial egg load difference, oviposition pre-experience, and host quality on females' relative number of attacks

Factors affecting females' aggressiveness	df	Estimates	F	P
Intercept		-1.94		
Egg load difference	1	0.01	1.064	0.31
Pre-experience (pupae)	1	1.83	0.24	0.63
Host quality (pupa)	1	1.61	0.0063	0.94
Egg load difference × pre-experience (pupae)	1	-0.025	0.012	0.91
Egg load difference × host quality (pupa)	1	0.17	1.15	0.29
Pre-experience (pupae) × host quality (pupa)	1	-2.86	9.73	<0.01
Egg load difference × pre-experience (pupae) × host quality (pupa)	1	0.089	0.047	0.83
Residuals	55			
Total	63			

P values of significant explanatory variables are highlighted in bold font.

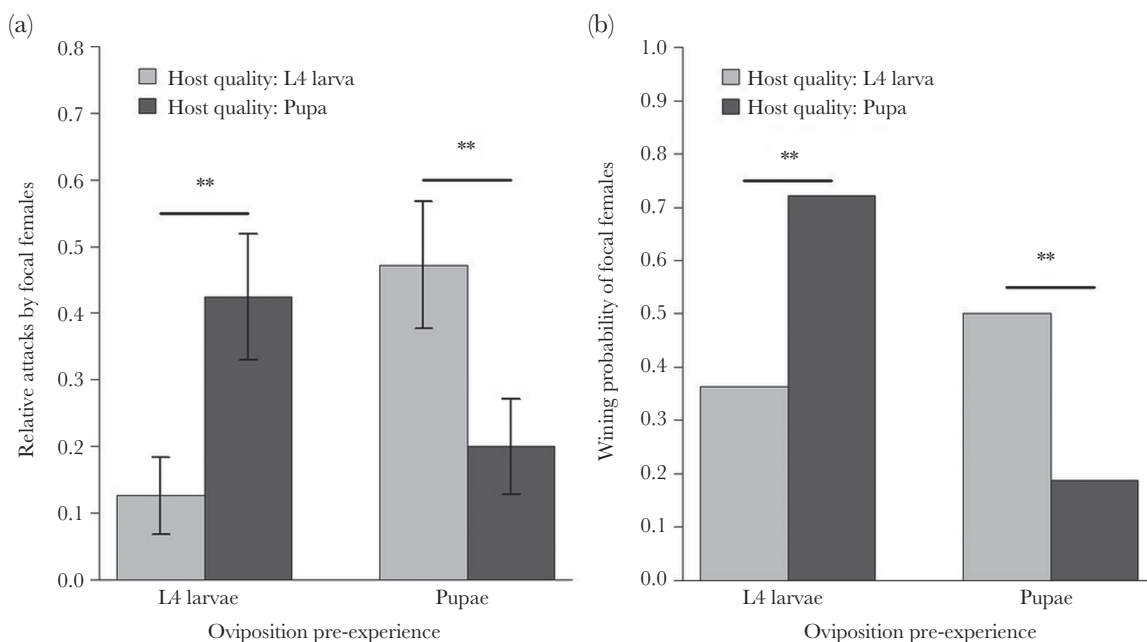


Figure 2

(a) Mean (\pm SE) relative number of attacks displayed by focal females with different oviposition pre-experiences when fighting for a L4 larva (gray bars; $n = 29$) or a pupa (dark gray bars; $n = 34$). (b) Probability of focal females with different oviposition pre-experiences winning a contest when fighting for a L4 larva (gray bars; $n = 29$) or a pupa (dark gray bars; $n = 34$). ****** $P < 0.01$.

outcome. Thus, wasps' agonistic behaviors and winning probability were influenced by the habitat quality they previously experienced, their number of ready-to-lay eggs and type of host being contested.

In our first experiment, the body mass of the offspring at emergence varied according to the type of host on which they developed: female offspring were heavier after developing on L4 larvae than on pupae. In parasitoids, like in many insect species, adult body mass usually correlates positively with fitness because heavier individuals often live longer and are more fecund (Honěk 1993; Visser 1994; Ueno 1999; Sokolovska et al. 2000; Rivero and West 2005; Lacoume et al. 2006). This result therefore suggests that L4 larvae represent higher-fitness hosts for mothers than pupae. However, as *C. maculatus* larvae were also heavier than pupae (Student paired-test: $t = 4.55$, $P < 0.001$), we cannot disentangle whether the benefits derive from the hosts' developmental stage or their mass.

Because of the positive correlation between host quality, individual body mass, and fitness in parasitoid offspring, the primary selection pressure driving the evolution of parasitoids is often seen as the one maximizing the adult size of these offspring, and mother oviposition strategies have been presumed to maximize this trait (Visser 1994). As such, we expected *E. vuilleti* females to benefit more from ovipositing on higher-quality hosts, mainly when they were deprived of such hosts (i.e. they came from a low-quality habitat). It was therefore surprising to find that neither the objective host value nor the oviposition pre-experience affected oviposition decisions: females laid first on the first host they encountered in their environment. Some may argue that these wasps were not able to assess the developmental stage of the host they parasitize, hence being unable to adjust their behavior accordingly. This seems unlikely because several studies in *E. vuilleti* already have demonstrated that females possess fine-tuned discrimination abilities. As shown in several other parasitoid species (see Visser et al. 1992; Jaloux et al. 2004; Todoroki and Numata 2017 for examples), *E. vuilleti* females are known to modulate their oviposition according to host condition

Table 3
Effect of the difference in females' initial egg load, oviposition pre-experience, and host quality on contest outcomes

Factors affecting contest outcomes	df	Estimates	G	P
Intercept		-0.77		
Egg load difference	1	0.42	8.16	<0.01
Pre-experience (pupae)	1	0.79	2.91	0.09
Host quality (pupa)	1	2.31	0.0001	0.99
Egg load difference × pre-experience (pupae)	1	-0.51	1.63	0.20
Egg load difference × host quality (pupa)	1	0.6	7.73	<0.01
Pre-experience (pupae) × host quality (pupa)	1	-5.25	10.68	<0.01
Egg load difference × pre-experience (pupae) × host quality (pupa)	1	0.95	0.9	0.34
Residuals	55			
Total	62			

P values of significant explanatory variables are highlighted in bold font.

(i.e. healthy vs. parasitized), as well as after detecting differences in the timing from the last oviposition (Leveque et al. 1993; Jaloux et al. 2004). Secondly, by providing hosts of different developmental stages (i.e. pupae, L4 larvae, or 3rd instar larvae) independently to 3 *E. vuilleti* females groups, Terrasse and Rojas-Rousse (1986) observed that the number of eggs laid by females increased with the developmental stage of their hosts: wasps in the presence of pupae laid more eggs than those provided with L4 larvae and they laid more eggs in the presence of L4 larvae than those provided with 3rd instar larvae. Finally, in our second experiment, female agonistic behaviors depended on the host type, demonstrating that they can discriminate between them. The lack of variation in female oviposition behavior in our first experiment may come from the fact that we minimized their threshold in host selectiveness. In a wide range of animal species, individuals from habitats where high-quality resources are scarce benefit more from choosing lower quality resources than from nothing, and thus tend to be less selective (Werner and Hall 1974; Stamps et al. 1981; Shelly and Bailey 1992; Gallant et al. 2004; Goubault et al. 2007a). We exposed wasps to only 1 host daily before starting behavioral observations. Mohamad et al. (2010) have previously noticed that females with many ready-to-lay eggs perceived such condition as a poor habitat in terms of host availability. In this context, laying eggs on 2 hosts of both types rather than on only 1 host of 1 type may be more advantageous for mothers.

In our second experiment investigating the role of both objective and subjective host value on female aggressiveness and contest outcome, our findings support studies showing that reproductive state asymmetry (i.e. subjective RV) greatly influence behavioral decisions during fights (Neat et al. 1998; Stokkebo and Hardy 2000; Arnott and Elwood 2008). Like Mohamad et al. (2010, 2012), we found that gravid females (i.e. with more mature eggs) have a higher probability of winning contests, hence confirming that asymmetry in initial egg load (a component of subjective RV) between contestants plays a main role in conflict resolution in *E. vuilleti*. We can explain this result by the fact that females with more developed reproductive tissue should place a greater value on host: they are more prepared to oviposit and should therefore be more likely to win access to the resource (Stokkebo and Hardy 2000). However, we also observed that the effect of initial egg load asymmetry between winner and loser females was less pronounced when the challenged host was a L4 larva (i.e. a high-quality host)

than a pupa. We assume that benefits to oviposit increased with the host quality (i.e. the objective RV) so that wasps with lower initial egg load (i.e. females placing a low subjective RV in hosts) would be more favored during contests for a L4 larva than for a pupa.

Furthermore, we showed that oviposition pre-experience (another component of the subjective RV) affected female aggressiveness and conflict resolution. Low-quality habitat females, which were deprived from high-quality hosts (i.e. females placing a high subjective value on hosts), were more aggressive when fighting for a high-quality host than those that previously experienced oviposition on such hosts and were more likely to win. This result is in accordance with both our expectations and theoretical predictions because the effect of subjective RV asymmetry is known to influence individual aggressiveness and conflict resolution in various contexts (Maynard Smith and Parker 1976; Hammerstein 1981; Enquist and Leimar 1987; Arnott and Elwood 2008). For example, males of the house cricket that were deprived of access to females were more aggressive and mated more often when competing for a female (Brown et al. 2006, 2007), whereas Dissanayake et al. (2009) showed that starved male shore crabs *Carcinus maenas* fought more and were more likely to win access to a cockle on which they feed. In the gregarious parasitoid wasp *Goniozus legneri*, both objective (host size) and subjective (contestant age) components of RV additively affected contest intensity (aggressiveness) for hosts: females competing for larger hosts and older contestants behaved more aggressively (Stockermans and Hardy 2013). However, to our knowledge, the present study is the first one to describe an interactive effect of both objective and subjective components of RV in a situation of intraspecific competition.

Surprisingly, we found females with oviposition pre-experience on L4 larvae to be more aggressive and to win fights more frequently to access a pupa (i.e. a low-quality host). On one hand, female host-feeding capacity may explain their greater host-acquisition abilities. In parasitoid species, host haemolymph is an available resource for both reproductive and metabolic needs (Jervis and Kidd 1986; Giron et al. 2002). Here, to feed on L4 larvae (i.e. heavier hosts) may imply higher energy intake for high-quality habitat females compared with low-quality habitat females that only host-fed on pupae (Lawrence 1990; Godfray 1994). Because their egg maturation did not increase, wasps may have converted this energy into host searching/exploitation ability. Moreover, mothers from low-quality habitat may have not fed on hosts of reduced size such as small pupae because hosts also serve for the development of their offspring. Concurrent host-feeding and oviposition behaviors on the same host has been observed to render hosts less suitable for offspring development (Heimpel and Rosenheim 1995; Ferracini et al. 2006); it may have been more advantageous for mothers to only lay in this situation. As a result, females that experienced a habitat with high-quality hosts would therefore have had a higher energy level (i.e. a higher RHP) at the beginning of the contest than those that experienced a low-quality habitat. RHP asymmetry may have overcome subjective RV asymmetry in this case. This agrees with Goubault et al. (2007a) who found in *P. vindemmiae*, another parasitoid species that host feeds, that females from rich habitats (high host availability) were advantaged during contests. Although L4 larvae allowed the development of heavier daughters, pupae may allow the development of offspring with advantageous fitness traits we did not measure in our study, so that mothers would benefit from ovipositing on both host types. For example, larval and pupal stage of many holometabolous insect hosts such as *C. maculatus* have different endocrine and metabolic profile that greatly

affect parasitoid fitness (see Lawrence 1990 for a review). Mondy et al. (2006) showed that variation in cholesterol level, acquired via host feeding during development, played a crucial role for egg viability in newly emerged *E. vuillei*. If both types indeed represent resources with different benefits for offspring (i.e. both host types have high objective RV), this would explain why, in the first experiment, mothers laid their eggs on the first encountered host. Moreover, deprivation of one host type may have increased the value that females place on it (i.e. higher subjective RV), which, in this case, could have led females to be more aggressive and more likely to win. We need further investigations to identify any benefits newly emerged wasps may have acquired through developing on a pupal host.

CONCLUSION

By testing the role of initial egg load, previous habitat quality, and host quality on female agonistic behaviors and probabilities of winning contests over host, we have shown for the first time that both objective and subjective RV interact to influence the intensity (aggressiveness) and the resolution of conflicts for indivisible resources. Our study highlights that the relationship between key factors affecting intraspecific competition may be more complex than expected. We thus call for further investigations of the interactive effects of the different components of RV on animal contests and their resolution.

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