Lethal male–male combat in the parasitoid *Melittobia acasta*: are size and competitive environment important?

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Interactions between organisms can lie anywhere along the spectrum from fatal conflict to total cooperation. To understand this variation, knowledge of the strategies that individuals use to acquire their resources is required. We tested theoretical predictions relating to conflict behaviour in a species of parasitoid wasp, *Melittobia acasta*, in which males compete for mates in their closed, natal patches. They engage in lethal combat to gain access to the females developing in their host. Environmental factors and individual traits both influenced conflict behaviour and contest outcome: fighting behaviour increased with the density of competitors and larger contestants were more successful. Our results also indicate that opponent assessment did not influence conflict behaviour and contests were always resolved by fighting.

When individuals come into conflict, the outcome may lie anywhere on the spectrum between peaceful resolution and escalated violence. For example, male pied wagtails, *Motacilla alba*, defend their territories peacefully by calling (Davies & Houston 1981), whereas male fig wasps will fight viciously in competition for mates (Hamilton 1979). How can this variation be explained? In particular, given that fighting can lead to injury and even death, why should it ever be favoured (Enquist & Leimar 1990)? Theory predicts that the way in which conflict is resolved will depend upon the relative costs and benefits of fighting, with escalation to violence predicted in situations where the benefits of winning are relatively high (Maynard Smith & Price 1973; Enquist & Leimar 1990).

Numerous factors are predicted to alter the costs and benefits of fighting, and hence determine the occurrence, frequency and severity of escalated contests (Murray 1987; Enquist & Leimar 1990; Anderson et al. 2003; Gammell & Hardy 2003; Taylor & Elwood 2003; Batchelor et al. 2005). A useful distinction can be made between those factors describing variation in an individual's environment and those relating directly to variation in traits of the interacting

individuals (such as size, experience, age and motivation). Important environmental variables to consider include the number and density of competitors, the availability and value of the contested resource, and the relatedness between competitors (Murray & Gerrard 1985; Enquist & Leimar 1987; Murray 1987; West et al. 2001, 2002). Conflict is predicted to escalate when conditions are such that the value of a resource at the present time is much greater than any potential future value of the resource (Enquist & Leimar 1990). Wingless male fig wasps will fight violently when there are few females within the same fruit, as they represent a limited number of future mating opportunities; conversely, when females are numerous their relative value is lower so the level or intensity of fighting is reduced (West et al. 2001).

The cost:benefit ratio of fighting will also be influenced by an individual's relative fighting ability, since this will affect contest outcome. For example, large, high-quality individuals may be more likely to fight over a resource, particularly when in competition with a smaller individual (Maynard Smith & Price 1973). Assessment rituals may mediate the escalation of conflict (Enquist & Leimar 1983, 1987; Leimar & Enquist 1984; Gammell & Hardy 2003; Taylor & Elwood 2003). In some cases, individuals assess their own competitive ability, for example orb-weaving spiders, *Argyrodes antipodiana* (Whitehouse 1997; Bridge et al. 2000; Taylor et al. 2001) and fiddler crabs, *Uca*

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mjoebergi (Morrell et al. 2005). In others, mutual assessment occurs, for example in the common toad, *Bufo bufo* (Davies & Halliday 1978), cichlid fish, *Nannacara anomala* (Jakobsson et al. 1979) and red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979). In contrast, when opponents are more evenly matched in size or quality, there is a much higher chance that conflict will escalate to violence.

Our aim was to test theoretical predictions about the nature of conflict and the factors influencing contest outcomes, using the parasitoid wasp *Melittobia acasta*. Males fight to the death, presumably because of the limited mating opportunities available within their natal host pupae, and as such provide a useful system for investigating conflict (Griffin & West 2002; Abe et al. 2003b, 2005; Innocent et al. 2007). We first considered environmental factors that may influence the outcome of conflict between males. We manipulated the density of opponents, the number of available mates and, thus, the operational sex ratio of the competitive environment. We predicted that the level of fighting will rise with (1) increasing male density, because this will lead to more frequent encounters between males (Murray 1987; also see Discussion), and (2) decreasing female density, because this increases the value of any particular female (Enquist & Leimar 1990; West et al. 2001). We then focused upon traits related to individual fighting ability. We searched for evidence of opponent assessment mediating fighting behaviour by testing whether fights were more likely to occur between size-matched than asymmetric opponents. We then investigated how variation in individual fighting ability influences the outcome of contests by testing whether large males competed more successfully.

METHODS

Life History and General Methods

The eulophid wasps in the genus *Melittobia* are gregarious Hymenopteran parasitoids with a worldwide distribution (González et al. 2004). The only species of *Melittobia* found in Europe is *M. acasta*, and this species is also prevalent in parts of North and South America, Japan, India, Australia and New Zealand (González et al. 2004). *Melittobia acasta* is a generalist parasite, able to parasitize a wide variety of hosts, including species of Hymenoptera, Diptera, Lepidoptera and Coleoptera (Balfour Browne 1922; Dahms 1984; González et al. 2004).

Our U.K. population was collected in the field in 2004 by M. Shaw (Royal Museum of Scotland, Edinburgh, U.K.) from solitary hymenopteran pupae, and subsequently cultured in the laboratory on *Calliphora vomita* pupae. Our stock culture methods result in the clutches of several females developing in the same host and several hundred wasps can successfully emerge from a single host. For each generation we housed approximately 60 females in glass vials, stoppered with cotton wool, and provided them with about 20 hosts to oviposit upon throughout their lifetime. We reared stocks at 30°C; at this temperature eggs develop into adults in about 13 days, with males emerging from pupae 1–2 days before females (Buckell 1928; Dahms 1984; Innocent et al. 2007). Eggs hatch 4–5 days after oviposition, larvae pupate after 7 days and males emerge as blind adults after 11–12 days (Balfour Browne 1922; Buckell 1928; Innocent et al. 2007). Upon emergence, males attack each other, using their mandibles to chop off their opponents' genitals, head and appendages; the victors then mate with females as they emerge from their pupal case (Buckell 1928; van den Assem et al. 1980; Dahms 1984; Innocent et al. 2007). Females are normally long winged, have eyes, and after mating disperse to new hosts to lay their eggs, whereas males do not leave their natal patch. Females lay large clutches (up to about 250 eggs) in their lifetime (Balfour Browne 1922), and, as they are haplodiploid, can produce daughters by fertilizing eggs and sons by laying unfertilized eggs. To produce experimental males, we opened up host pupae 10 days after oviposition, and dissected out virgin female pupae. As virgin females can lay only sons, we used them to produce large numbers of males.

Experiment 1: Competitor Density

In experiment 1, we manipulated the number of opponents and available mates and, thus, the operational sex ratio (OSR; proportion of adult males) of the competitive environment. For each competitive environment we measured whether males were engaged in combat or courtship behaviour. To produce males in large quantities, we kept virgin females in groups of about 100 and provided them with about 30 hosts. We opened hosts at 10 days after oviposition, and virgin male pupae were isolated and stored individually in gelatin capsules. We stored males at 30°C until emergence and randomly allocated each male to a contest arena. Within 24 h of emergence, we added males and virgin females to their contest arenas, which consisted of gelatin capsules (with similar dimensions to *Calliphora* host pupae: volume = 0.21 ml). We cross-factored arenas for the number of competitors (male number) and the number of mates (female number). Male number had three levels (1, 2 and 8 males) and female number had five levels (0, 2, 8, 36 and 100 females). We chose these values to span the spectrum observed emerging from our stock-producing hosts and to represent OSRs of 0.01–1. We refrigerated both males and females at 5°C for 10 min to immobilize them long enough for the correct number to be counted and added to each arena. We set up 10 contest arenas per treatment combination for two and eight males, and five per single-male combination. We monitored each arena under a dissecting microscope, and counted males engaged in combat or courtship behaviour after 5 min, per arena. We classed behaviour as being either combat (interaction between two or more males) or courtship (interaction between a male and female including mounting, abdomen exploration, antennal clasping and copulation). After this, we refrigerated each arena for 5 min to immobilize the animals, and transferred them to a 1.5-ml microfuge tube, which was stoppered with cotton wool and masking tape. We incubated the tubes at 30°C, and checked them

at intervals of 2, 4, 24, 48 and 72 h, to record when the first male in each arena died. We used microfuge tubes because, once mated, females will chew their way out of gelatin capsules to disperse from their 'natal' patch.

Experiment 2: Body Size

In this experiment, we investigated how variation in individual body size influences contest outcome, and whether asymmetry in this trait can influence the probability and outcome of combat. We created different-sized males by manipulating the level of larval competition experienced during development. We created large males by giving groups of 30 virgin females 40 fresh hosts in a stoppered glass tube. This created an environment with a low density of competitors, and resulted in low resource competition. Conversely, we created small males by giving groups of 30 virgin females only one fresh host. We opened all hosts 10 days after oviposition, isolated the male pupae, and stored them individually in gelatin capsules. We used a dissecting microscope to photograph each male pupa and Leica IM50 measurement software (Leica, Wetzlar, Germany) to measure the head width, body length and mandible length for each male. By measuring pupal traits, we avoided measurement error introduced from attempting to photograph emerged males in a stationary and standard position. We initially measured the length of both mandibles, but as there was no significant asymmetry in the right and left mandible lengths (Student's t test: $t_{27} = 1.02$, $P = 0.318$), we measured only left mandible length for subsequent pupae. We stored measured males in individual gelatin capsules at $30°C$ until they emerged. Within 24 h of emergence, we randomly allocated our measured, virgin males to 30–60 replicates for each of three different contest categories: large versus large; small versus small; or small versus large. We marked each male on his abdomen with either pink or gold paint, and colour was cross-factored with contest category. We set up contest arenas by adding the opponents to a gelatin capsule with approximately the same dimensions as *Calliphora* host pupae (volume = 0.21 ml). We observed all arenas for 30 min after set-up, and counted the fights. We recorded a fight when males made contact with each other and began to fight. If contact between the opponents was made, but there was no escalation, we did not record a fight. We checked arenas every 24 h, and the first male to die in each arena was recorded as the loser. We also set up arenas with single, marked males for each size treatment, and recorded longevity.

Statistical Analysis

For maximum power when analysing proportion data, analyses should assume binomial errors and use a logit link function, as proportion data often have non-normally distributed error variance and unequal sample sizes (Crawley 1993, 2002; Hardy & Field 1998). In this case, analyses using generalized linear models (GLMs) are simplified by using analyses of deviance, in which changes in deviance are compared to a chi-square distribution. However, proportion data can be overdispersed (residual deviance > residual degrees of freedom), and this can lead to overestimation of significance. If the dispersion parameter (heterogeneity factor; HF) is <4, the chi-square distribution should not be used but data can be scaled and F tests used to assess significance (Crawley 2002). We carried out our analyses using R version 2.1.0 (The R Foundation for Statistical Computing, Vienna, Austria). We used binomial errors and chi-square distributions in cases where HFs were <1 and quasibinomial errors and F distributions when HFs were >1 but <4. For parametric data we used GLMs with normal errors where possible and Kruskal–Wallis tests for nonparametric data.

RESULTS

Experiment 1: Competitor Density

Combat behaviour

We were able to record combat data from all of the two- and eight-male contest arenas that we set up. The proportion of males engaged in combat was significantly greater in arenas with more males (GLM: $F_{1,99} = 13.12$, $P = 0.0005$; Fig. 1a), and this decreased with the density of females ($F_{4,99} = 7.96$, $P = 0.0001$; Fig. 1a), but there was no significant interaction between male and female density. These results are supported by further analysis showing that the proportion of males engaged in combat increased with the OSR ($F_{1,99} = 14.78$, $P = 0.0002$; Fig. 1b).

Courtship behaviour

We were able to record courtship data from all of the one-, two- and eight-male contest arenas that we set up. The proportion of males that were courting or mating was significantly greater in arenas with fewer males (GLM: $\chi_2^2 = 32.35$, $N = 125$, $P < 0.0001$; Fig. 2a), and increased with female number ($\chi_2^2 = 152.15$, $N = 125$, $P < 0.0001$; Fig. 2a). These results are supported by further analysis showing that the proportion of males courting decreased as the OSR increased ($\chi_2^2 = 165.89$, $N = 125$, $P < 0.0001$; Fig. 2b).

Longevity

The median longevities for single males and those in one-, two- and eight-male arenas were 100, 72 and 24 h, respectively. The life span of the first male in each arena to die had a significant negative association with the number of males present (GLM: $\chi_3^2 = 377.98$, $P < 0.0001$).

Experiment 2: Body Size

Male size manipulation

Our larval competition treatments successfully created males that were significantly different in size (Table 1). Males from the low-competition treatment had significantly longer bodies (GLM: $F_{1,111} = 35.50$, $P < 0.0001$), wider heads ($F_{1,111} = 44.18$, $P < 0.0001$) and longer
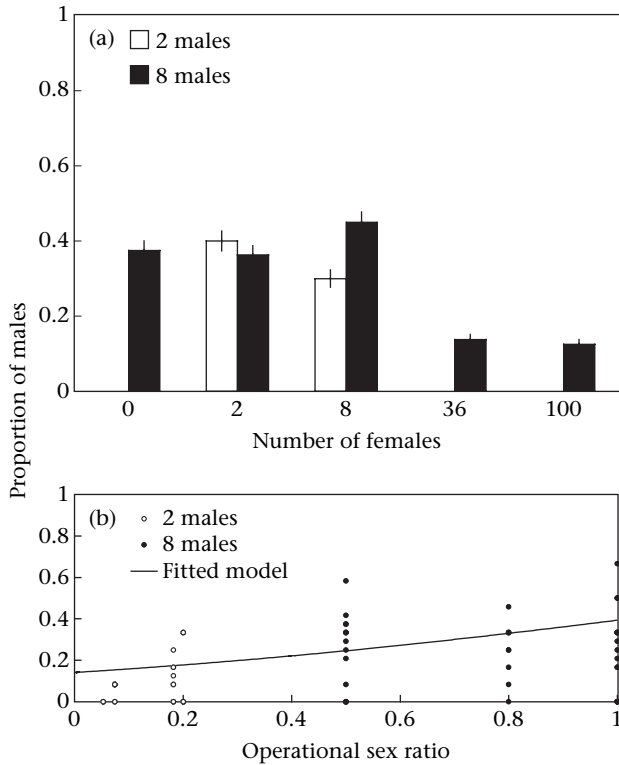
Figure 1. (a) The mean ± SE proportion of males engaged in combat after 5 min in arenas containing different numbers of opponents and mates. (b) Proportion of males engaged in combat after 5 min in relation to the operational sex ratio (OSR; proportion male). We fitted the line from the logistic regression model, proportion fighting $= e^{(a + bx)}/1 + e^{(a + bx)}$ where $a = -1.808$, $b = 1.375$ and $x = $ OSR.

mandibles ($F_{1,111} = 23.62$, $P < 0.0001$) than males in the high-competition treatment.

Asymmetries in body size

Of the 120 contest arenas that we set up, 114 (95%) had a clear winner. The number of fights observed in the first 30 min was not significantly different between large size-matched, small size-matched and asymmetric contests (GLM: $\chi_2^2 = 1.95$, $P = 0.377$). This suggests that males do not assess their own competitive ability or that of their opponent. The colour of marks applied to males did not influence the probability of winning fights (57 pink and 57 gold males won fights; binomial test: $P = 1.00$), so we chose gold males as our focal individuals. We used the probability of a gold male winning, P(winning), as our GLM response variable, thus allowing size data to be fitted as explanatory terms (Hardy & Field 1998). When size was fitted as the relative difference between the focal male and his opponent (i.e. the focal male was either smaller, the same size or larger), larger males were significantly more likely to win contests (GLM: $\chi_2^2 = 47.4$, $N = 114$, $P < 0.00001$).

Asymmetries in specific traits

We calculated the absolute differences in body length between each focal male and his opponent, and found that the probability of the larger male winning increased
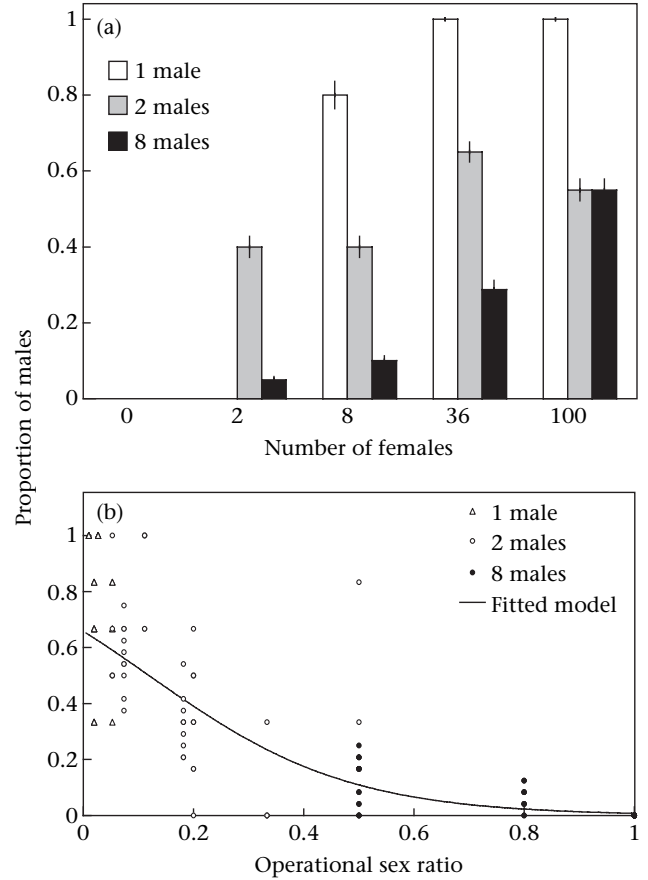

Figure 2. (a) The mean ± SE proportion of males engaged in courting or mating after 5 min in arenas containing different numbers of opponents and mates. (b) Proportion of males engaged in courting or mating after 5 min in relation to the operational sex ratio (OSR; proportion male). We fitted the line from the logistic regression model, proportion courting $= e^{(a + bx)}/1 + e^{(a + bx)}$ where $a = -0.656$, $b = -5.505$ and $x = $ OSR.

with the asymmetry in body size of opponents (GLM: $\chi_1^2 = 66.47$, $N = 114$, $P < 0.0001$; Fig. 3). The absolute differences in body length, head width and mandible length were significantly and positively correlated with each other (all $R^2 > 0.95$, $P < 0.0001$). Therefore, to establish the influence of head width and mandible length on contest outcome, we controlled for body size by using as our response variable the residuals from the logistic regression analysis between body size and the probability of winning

Table 1. Means and 95% confidence intervals (CI) of the sizes (mm) of males in the large and small treatments in experiment 2

	Large males		Small males	
	Mean	95% CI	Mean	95% CI
Body length	2.508	(2.433, 2.585)	2.217	(2.143, 2.290)
Head width	0.685	(0.663, 0.708)	0.588	(0.566, 0.610)
Mandible length	0.123	(0.117, 0.128)	0.106	(0.102, 0.111)
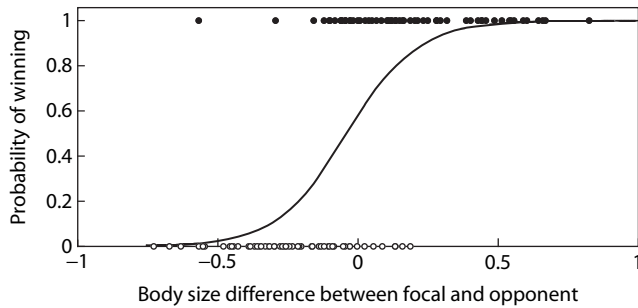
Figure 3. The probability of winning a fight in relation to the magnitude of the difference (mm) in body size of opponents. ●: Fights in which the focal male won; ○: fights in which the focal male lost. We fitted the line from the logistic regression model, P(winning) $= e^{(a + bx)}/1 + e^{(a + bx)}$ where $a = 0.318$, $b = 8.002$ and $x =$ size difference. In our experiment the mean difference in body size was about 0.3 mm, range 0.007–0.8 mm.

contests. We carried out separate analyses on these residuals for head width and mandible length to avoid problems associated with colinearity. When we controlled for body size, the probability of winning fights was significantly and positively correlated with the magnitude of the difference in head width: the larger a male was compared to his opponent, the more likely he was to win (GLM: $F_{1,111} = 6.31$, $R^2 = 0.05$, $P = 0.013$; P(winning) $= 0.009 + 2.22 \times$ difference). When we controlled for body size, males with larger mandibles were also more likely to win fights, and this increased as the difference in mandible lengths of opponents increased ($F_{1,111} = 5.67$, $R^2 = 0.05$, $P = 0.019$; P(winning) $= 0.0005 + 8.83 \times$ difference).

DISCUSSION

Our results support theoretical predictions concerning how the competitive environment should influence the level of fighting. Specifically, (1) greater male density led to more fighting (Fig. 1), less courting (Fig. 2) and shorter male life spans; (2) greater female density led to an increase in the proportion of time males spent courting/mating, and a decrease in the time spent fighting (Figs 1 and 2). Within contests, larger competitors were far more successful than smaller competitors (Fig. 3). Furthermore, when we controlled for body size, large head width and mandible size increased competitive ability (Innocent et al. 2007). Fighting was not more frequent when there was an asymmetry in fighting ability between opponents, which suggests that assessment did not mediate contest behaviour.

Variation in male density can have two effects, which influence fighting behaviour in opposing directions (Murray & Gerrard 1985; Murray 1987; Reinhold 2003). First, increased male density will increase the encounter rate between individuals. This is predicted to lead to more fights, as has been observed in the fig wasp *Philotrypesis pilosa* (Murray 1987). Our measure of fighting corresponds to fight frequency, and we found a similar pattern (Fig. 1). Second, male density alters the cost of fighting, and this is

also predicted to affect fight intensity (Murray & Gerrard 1985; Murray 1987; Enquist & Leimar 1990; Reinhold 2003). Specifically, increased density of competitors will decrease the benefit gained by fighting in any given fight, because: (1) fighting wastes time, as other males will be concurrently mating with females (Murray 1987); (2) the probability of beating all competitors decreases with time spent fighting (Reinhold 2003). Murray (1987) described the interaction between these opposing factors, such that the greatest overall fighting cost is found at intermediate male densities: fights are more numerous than at low densities and fiercer than at high densities. None the less, given the small number of males we used per treatment (1–8 males), we would still expect a positive correlation between density and cost of fighting over this range (see figure 2 in Murray 1987). High male densities could also lead to a reduction in the probability of initiating a fight (Reinhold 2003), but our observations suggest that, in the case of *M. acasta*, fighting will always occur. Hence, these predictions are not met; however, Reinhold (2003) also suggested that, if kin recognition were present, the effect of male density may change.

Given the high cost of fighting (death upon losing), we might expect to find evidence of opponent assessment (Enquist & Leimar 1983, 1987; Leimar & Enquist 1984). In particular, given that large size significantly improves competitive success, we might expect small males to avoid fighting (Petersen & Hardy 1996; Fig. 3). However, behavioural observations suggest that *M. acasta* males always fight, and that fighting between two males begins immediately they encounter each other (S.E. Reece, unpublished data). There are two reasons why we might expect this to be the case. First, Enquist & Leimar (1990) showed that, if the value of the resource being contested is much larger than the value of potential future resources, all conflicts should be resolved by fighting rather than by retreating. In this case, it is not in the interests of weaker competitors to avoid a fight: even if the probability of winning is very small, as for *M. acasta*, there is a chance of winning, and this resource is extremely valuable. Put simply, males fight because they have little to lose and a lot to win (the 'desperado effect' Grafen 1987). Second, while models of fatal conflict assume that retreating is an option, *Melittobia* males may be unable to run away and thus have to fight. As male *Melittobia* are blind, tactile cues may be the only way to assess their opponents and close proximity may make fighting inevitable. The idea here is that the higher-quality male must ensure he kills the lower-quality opponent.

To conclude, this study and previous work on *Melittobia* species have identified a number of factors that may influence fighting behaviour. We have focused upon the effects of male and female density and body size on contest behaviour in *M. acasta*. Previous studies on *Melittobia australica* have shown that early emerging males will almost always kill pupal males upon eclosion, suggesting that early emergence confers a competitive advantage in lethal combat (Abe et al. 2003b; Innocent et al. 2007). Therefore, emergence order and body size have independent and striking effects on the probability of winning a fight, but their relative importance is unknown. It would be

extremely useful to examine the interplay between fighting ability (e.g. body size) and ecological factors (e.g. emergence order) as, in most cases, competitive ability is the overriding factor (Petersen & Hardy 1996; Batchelor et al. 2005; Innocent et al. 2007). Furthermore, understanding the dynamics of fights between males could help explain the unusual lack of sex ratio adjustment that has been observed in *Melittobia* species, in response to the number of females laying eggs in a patch (Abe et al. 2003a, b, 2005; Cooperband et al. 2003; Matthews et al. 2005). For example, if later-born males are killed by previously emerged males, then the relative fitness of producing males late in a brood are reduced and so the offspring sex ratio (proportion males) is not expected to increase as more females lay eggs on a patch (Abe et al. 2003a, b, 2005; Shuker et al. 2005; Innocent et al. 2007).

Acknowledgments

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