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Robert W. Matthews
University of Georgia

Leif D. Deyrup
DHHS

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**FEMALE FIGHTING AND HOST COMPETITION
AMONG FOUR SYMPATRIC SPECIES OF *MELITTOBIA*
(HYMENOPTERA: EULOPHIDAE)**

Robert W. Matthews¹ and Leif D. Deyrup²

ABSTRACT

Melittobia is a genus of parasitic wasps well known for high levels of inbreeding and violent male combat. Casual observations of groups of sisters of *M. femorata* placed with hosts revealed a surprising incidence of body mutilations (broken or missing tarsi, antennae, and wings). Replicated conspecific groups of 1, 2, or 3 females of *M. femorata*, *M. digitata*, and *M. australica* and interspecific groups of *M. femorata* and *M. australica* (2:1) were observed over their first 10 days in newly established cultures, and the incidence of mutilation was recorded. In some groups females were dye-fed, allowing us to subsequently chart their individual activity patterns on or near the host based on patterns of their colored fecal droppings. For *M. australica* and *M. digitata*, no conspecific females in any group size ever showed mutilation. However, in *M. femorata* nearly 3/4ths of the females in conspecific groups of two or three acquired body damage beginning about the time of first oviposition on the host. In 4 of 5 replicates of the interspecific groups, *M. femorata* females killed the female of *M. australica*. Patterns of dyed fecal droppings that developed over several days showed that individual females in groups of both *M. femorata* and *M. australica* increasingly restricted their activities to a small portion of the host. These "micro" territories were non-overlapping and appeared to be actively defended. In contrast, *M. digitata* females in groups never displayed obvious territoriality or interference. Possible reasons for these differences in female behavior are discussed.

Melittobia are small external parasitoids that attack solitary bees, wasps, and their associates (Balfour-Browne 1922, Buckell 1928, Dahms 1983b, Krombein 1967). This cosmopolitan genus includes 12 species, some of which coexist geographically, often upon the same hosts (Matthews et al. 2009). Across eastern North America, a common shared host is the mud-dauber wasp, *Trypoxylon politum* Say (Hymenoptera: Sphecidae). Another common host sphecid, *Sceliphron caementarium* Drury, coexists with *T. politum*, but extends its range to include the western United States.

All *Melittobia* species appear to have a generally similar life history. Upon finding a host prepupa, the female parasitoid stings it and feeds upon exuded host fluids. This stimulates egg maturation and within 2 to 4 days, she begins to oviposit on the host; over the ensuing 10 days, she ultimately may lay hundreds of eggs in clusters on individual large hosts.

Most of these eggs develop into female offspring, either of an early brachypterous form or a later macropterous dispersal form (Schmieder, 1933, Cònsoli and Vinson 2002). Males, which generally comprise 5% or less of the offspring, emerge at a low but continuous rate throughout female emergence (Adams

¹Dept of Entomology, University of Georgia, Athens, GA 30602. (e-mail: rmatthew@uga.edu).

²DHHS/Maine CDC, Division of Infectious Disease, 286 Water Street, Augusta, ME 04333.

2002). Before dispersing, the females mate with these males, which are very likely brothers; thus, inbreeding appears to be the usual situation.

Males of *Melittobia* are known for their lethal combat (Hamilton 1979, Hartley and Matthews 2003, Deyrup et al. 2006, Innocent et al. 2007). Females, however, are generally considered docile and even supportive of one another; for example, *M. digitata* females non-aggressively queue up to await male courtship and cooperate with one another to chew out of the host's nest. (Donovan 1976, Deyrup et al. 2005). This female docility may not be the rule, however. Much of the available information on *Melittobia* is based on research conducted with this one species that is sold under the name "WOWBug" (Carolina Biological Supply Co., Burlington, NC). Because of its ready availability and ease of rearing on artificial hosts such as the common blowfly, *Sarcophaga (Neobellieria) bullata*, *M. digitata* is becoming a model organism for laboratory and classroom work. However, two less-studied species, *M. femorata* Dahms and *M. australica* Girault, are actually the most commonly collected *Melittobia* species on *T. politum* in the southeastern United States (J.M. González and R.W. Matthews, unpublished data). Also sympatric but generally more northerly and less widespread is *M. acasta* (Walker), which may have been accidentally introduced from Europe by way of Canada at least 40 years ago (González et al. 2004).

The extent of parasitoid competition in arthropod communities is unresolved, but thought to be widespread (Godfray 1994, Hawkins 2000), especially since multiple species often attack the same host. Competition may be manifested in various ways and at different times in the parasitoid-host interaction. Both interference and exploitative competition can occur and there are numerous examples, especially from the biological control literature (Hawkins 2000). Several parasitic wasps have been reported to defend a host resource, their eggs, or their offspring from conspecifics (e.g., Field and Calbert 1999, Hardy and Blackburn 1991, Wilson 1961). Interactions among female parasitoids often are mediated via chemical markings that appear to deter conspecific females from superparasitism (Hoffmeister and Roitberg 1997, Petersen and Hardy 1996). Among host searching female ectoparasitoids, competition between congeneric species has been little studied.

In our laboratory on various occasions we have noted both intra- and interspecific aggression, body damage, and death when combinations of *Melittobia* females have been placed on a common host. Field collections of host *T. politum* cocoons have revealed natural multiparasitism by two or rarely three *Melittobia* species on at least five occasions: three from Georgia, and one from both Alabama and New York (González and Matthews, unpublished data). Thus, to better understand competitive interactions among host-seeking females we undertook the studies reported here.

MATERIALS AND METHODS

All four *Melittobia* species were originally obtained from parasitized cocoons of the mud dauber wasp, *Trypoxylon politum* Say (Hymenoptera: Sphecidae). The *M. femorata* stock originated from Arnoldsville, Oglethorpe Co., GA; *M. digitata* from Athens, Clarke Co., GA; *M. australica* from Gainesville, Alachua Co., FL; and *M. acasta* from Townsend, Blount Co., TN. Prior to this study, laboratory cultures of each species had been continuously maintained from one to four years at the University of Georgia. Reculture protocol for each new generation was to haphazardly select five mated females of unknown age and place them on a naked *T. politum* prepupa in small vials maintained in a dark incubator at 25°C. New cultures were established every 21 days except for *M. femorata* whose reculture cycle varied from 90-120 days.

All experiments and controls used 1 to 2-day-old mated females that had eclosed from a single stock culture of each species. As hosts for these parasitoids,

we used naked *T. politum* prepupae extracted from local field-collected nests and individually placed in small plastic boxes (50 mm × 25 mm × 18 mm, Carolina Biological Supply Co., Cat. No. ER-14-4584). Experiments were conducted in the same individual plastic boxes and were maintained in a constant-temperature chamber at 25°C.

For some studies, we marked individual females by feeding them 20% fructose and water dyed with McCormick® food coloring. After females imbibe this fluid, it is easily visible in their crops through their semi-translucent cuticle (see Matthews et al. 2009); different colors served to identify individual females. In addition, because the color is retained in the female's fecal matter, this technique allowed us to track each female's activity through the pattern of her fecal droppings on the floor of the plastic box.

Female competition in *M. femorata*. In 28 boxes, mated 2-day-old unfed *M. femorata* females of the long-winged morph were concurrently placed with individually boxed *T. politum* prepupae in the following design: A single female in 6 boxes, 2 females in 13 boxes, and 3 females in 9 boxes. Boxes were maintained at ambient room temperatures and checked daily over the following 10 days, noting the females' behavior and recording any body damage. In order to track individual females and their movements, 15 additional cultures were established with 3 females of *M. femorata* marked by dye-feeding as outlined above.

Interspecific competition in *M. femorata* and *M. australica*. To determine how *M. femorata* fared when confronted with another species on the host, we set up five boxes containing one dye-fed *M. australica* and two dye-fed *M. femorata*. These boxes were observed daily for 10 days and body damage and fecal dropping patterns were recorded. For comparison with intraspecific competition between individuals, we concurrently set up 20 boxes of three dye-fed *M. digitata* females and 20 boxes of three dye-fed *M. australica* females; *M. acasta* was unavailable for this comparison.

Female competition in *M. digitata*, *M. australica*, and *M. acasta*. To further examine these interactions, a subsequent experiment used unfed females in a design that examined inter- and intra-specific interactions in three *Melittobia* species by comparison with solitary females. Three treatments placed two females of different species on a naked *T. politum* host (average weight = 0.253g ± 0.060 SD) in the 3 possible combinations: *M. digitata* vs. *M. acasta*, *M. digitata* vs. *M. australica*, and *M. australica* vs. *M. acasta*. Another three treatments placed conspecific pairs of each of the three *Melittobia* species. Controls consisted of cultures of each species established by a single female. Each treatment and control was replicated 10 times. *M. femorata* was not available for these comparisons.

Each treatment replicate and associated control was checked daily for the first 8 days, then twice weekly for the next 10 days, noting oviposition, feeding, and "jousting." At day 18 all emerged adults were sexed and counted to assess the effects of inter- and intraspecific competition on fecundity and reproductive success relative to solitary foundress control cultures of each species at the same stage.

RESULTS

Intraspecific female competition. In the treatments containing three dyed *M. femorata* females, 1 to 4 days after being placed on a host the females' activities became increasingly localized, each focused upon a particular portion of the host's body. From the distribution patterns of dyed fecal droppings it was apparent that each female *M. femorata* was developing a more or less exclusive "micro" territory (Fig. 1), and that the boundaries between them were relatively distinct. Undyed females in the groups of two or three in the other set of cultures

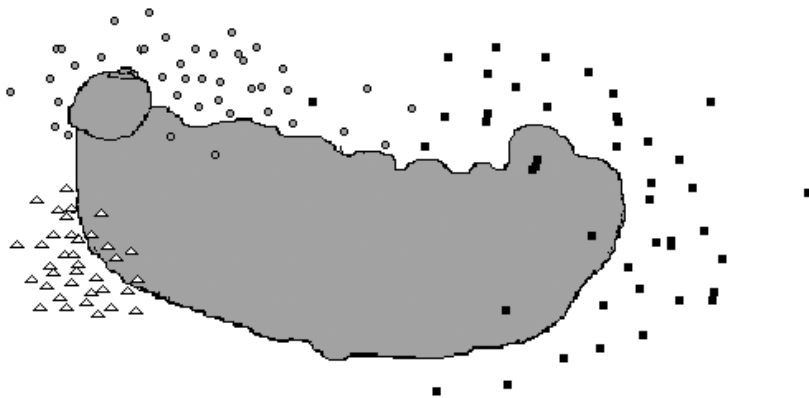


Fig. 1. The distribution patterns of accumulated dyed fecal droppings of three *M. femorata* females on a *Trypoxylon* prepupa 4 days after being placed together. The essentially non-overlapping "micro"territories or spheres of concentrated activity for each of these females is apparent. (Original green dyed droppings are represented as partially filled circles, red as filled squares and blue as unfilled triangles.)

appeared to behave similarly. Females of *M. australica* also displayed similar territoriality in all 20 cultures. However, fecal droppings of *M. digitata* females displayed no grouping pattern in any of the replicates.

During the course of oviposition (roughly days 2 -10), the frequency of aggression and incidence of body mutilation (manifested as missing tarsomeres and antennal flagellomeres and tattered and broken wings) increased among groups of *M. femorata* females. We regularly observed females biting at other females and even rolling around in locked combat (Fig. 2). In addition, many females were noted to walk about with their wings raised as though damaged. Normally, wings are held flat over their abdomens.

At least one female with damage occurred in every replicate (9/9 for groups of three females and 13/13 for groups of two females), and in several replicates all females in a group exhibited some type of body damage (Table 1). Overall, 16 of the 25 females in the foundress pairs replicates and 20 of the 25 females in the three foundress groups had body damage.

By contrast, none of the females in any of the 20 groups of three *M. digitata* or *M. australica* acquired body damage over the 10-day period. Periodic observation revealed no indication of agonistic interactions among females of *M. digitata*; however, while never overtly hostile, individual *M. australica* were sometimes seen to follow or approach other females on the host and appeared to disturb the other female with proximity or nudging.

Progeny production. In the final experiment, counts of adult progeny as of day 18 indicated that among both the single female control and the two conspecific female cultures, *M. digitata* was the most prolific, followed by *M. acasta* and *M. australica* (Table 2). Pair-wise interspecific comparisons of the average numbers of progeny produced showed that *M. acasta* outperformed both of the other two species when in direct competition, and that *M. digitata* did better than *M. australica*. However, *M. australica* was significantly less productive than either competitor (Tables 2 and 3). This contrasts to the intraspecific competition results where no significant differences in total progeny production were found between single female and two female cultures (Tables 2 and 3) though the variance in all experiments was great and the number of replicates relatively few.



Fig. 2. Two egg-laden female *M. femorata* locked in combat. Although these encounters do not tend to be lethal, females often mutilate one another.

Table 1. Incidence of damage among cofoundresses of *Melittobia femorata* in different sized foundress groups during the first 10 days of their being simultaneously placed with a *Trypoxylon politum* prepupa host.

Initial No. of females	No. of replicates with female damage/Total No. of replicates	Total No. of females*	
		With body damage	Without body damage
1	0/6	0	6
2	13/13	16	9
3	9/9	20	5

*Discrepancy in total numbers due to loss of three females that escaped or were accidentally killed.

Table 2. Numbers of *Melittobia* emerging by day 18 from each interspecific, intraspecific, and single female treatment on *Trypoxylon politum* prepupae. Values are means \pm S. D.

Treatment (N)	<i>M. acasta</i>			<i>M. australica</i>			<i>M. digitata</i>		
	Females	Males	Total	Females	Males	Total	Females	Males	Total
<i>M. acasta</i> + <i>M. australica</i> (10)	230.8 \pm 54.4	17.3 \pm 6.3	248.1 \pm 56.0	20.6 \pm 41.8	2.1 \pm 4.0	22.7 \pm 45.7			
<i>M. australica</i> + <i>M. digitata</i> (10)				48.4 \pm 30.2	1.2 \pm 1.0	49.6 \pm 30.6	95.6 \pm 74.2	5.5 \pm 3.1	101.1 \pm 75.0
<i>M. digitata</i> + <i>M. acasta</i> (10)	297.7 \pm 149.6	11.2 \pm 6.0	308.9 \pm 150.2				213.6 \pm 128.4	2.8 \pm 2.9	216.4 \pm 127.9
<i>M. acasta</i> + <i>M. acasta</i> (9)	397.7 \pm 181.5	15.7 \pm 5.9	413.3 \pm 181.2						
<i>M. australica</i> + <i>M. australica</i> (9)				269.9 \pm 140.2	6.6 \pm 1.3	276.4 \pm 141.1			
<i>M. digitata</i> + <i>M. digitata</i> (8)							417.0 \pm 160.5	13.6 \pm 4.9	430.6 \pm 160.3
<i>M. acasta</i> (9)	285.6 \pm 90.7	14.9 \pm 5.6	300.4 \pm 89.7						
<i>M. australica</i> (6)				196.2 \pm 193.0	5.7 \pm 4.7	201.8 \pm 192.9			
<i>M. digitata</i> (9)							389.6 \pm 133.7	8.0 \pm 2.5	347.6 \pm 133.6

Table 3. Statistical comparisons of progeny production of three *Melittobia* species in the inter- and intraspecific experimental treatment groups. *P* values are for two sample assuming unequal variance *t*-test (2-tailed).

Experiment	Comparison	<i>P</i>
Interspecific		
<i>australica</i> & <i>digitata</i>	Total <i>digitata</i> vs. ave. of 2 <i>digitata</i>	0.007
	Total <i>australica</i> vs ave. of 2 <i>australica</i>	0.005
	Total of both vs 2 <i>australica</i>	0.030
	Total of both vs 2 <i>digitata</i>	0.001
<i>australica</i> & <i>acasta</i>	Total <i>acasta</i> vs ave. of 2 <i>acasta</i>	0.262
	Total <i>australica</i> vs ave. 2 <i>australica</i>	0.001
	Total both vs 2 <i>australica</i>	0.913
	Total both vs 2 <i>acasta</i>	0.049
<i>digitata</i> & <i>acasta</i>	Total <i>acasta</i> vs ave. 2 <i>acasta</i>	0.089
	Total <i>digitata</i> vs ave. 2 <i>digitata</i>	0.983
	Total both vs 2 <i>digitata</i>	0.225
	Total both vs 2 <i>acasta</i>	0.169
Intraspecific		
<i>M. digitata</i>	Single female vs 2 females	0.268
<i>M. acasta</i>	Single female vs 2 females	0.437
<i>M. australica</i>	Single female vs 2 females	0.120

Female competition: *M. femorata* and *M. australica*. In the mixed species cultures, *M. australica* often appeared to pressure a female of *M. femorata* to abandon her territory, and in some instances caused her to move completely off of the host early in their association. However, after the *M. femorata* became physogastric (abdomens swollen with eggs), the tables turned, and in four of the five replicates the *M. australica* female exhibited damage and was eventually decapitated. In only one case did *M. femorata* and *M. australica* appear to share the same area on the host, with no evidence of any body damage.

Interestingly, in the cultures co-housing *M. femorata* and *M. australica* females, the onset of microterritoriality in *M. femorata* seemed to be delayed (3-5 days after being placed on host) relative to its onset for a single foundress; unfortunately, small sample sizes obviate firm conclusions.

Female competition: *M. acasta* and *M. australica*. In 8 of the 10 replicates, apparent signs of fierce and fatal competition were observed in females of both species within six days after introduction upon the host. Evidence of battles included damaged heads, broken and missing tarsi, tattered wings, and immobility. By 10 days the *M. australica* female was killed by *M. acasta* in 7 replicates, resulting in the very low numbers of progeny realized by *M. australica* (Table 2). In the three remaining replicates in which battles were not extreme enough to lead to immobility or death, both species nonetheless showed signs of struggle.

Female competition: *M. digitata* and *M. australica*. Based on daily observations, *M. australica* appeared to dominate over *M. digitata* during the first 12 days of the study, as *M. digitata* suffered more injuries and mortality (The *M. digitata* female was apparently killed in 2 replicates during first 10 days; in one other replicate both females were found dead after 4 days with no evident body damage to either). In the remaining 7 replicates both females survived with no injuries or evident aggression, though the daily checks revealed that the *M. australica* female was more often on the host. However, by the measure of number of adult females produced by day 18 of the study (Table 2), *M. digitata* dominated with significantly more progeny by every measure (Table 3).

Female competition: *M. digitata* and *M. acasta*. When *M. digitata* and *M. acasta* shared a host, no aggression or body damage was observed between the females during the first 10 days. Both species realized high adult progeny production, averaging over 200 for *M. digitata* and nearly 300 for *M. acasta* (Table 2) and not significantly different from that realized in intraspecific competition (Table 3). Interestingly, in the heavy fighting that was observed between emerging males of these two species, *M. acasta* dominated, killing most *M. digitata*.

DISCUSSION

Territoriality has been widely documented in insects; however, much of the literature focuses on males in various forms of intrasexual selection (Baker 1983). Territoriality or intense intraspecific competition involving partitioning and defense of resources among conspecific female insects is relatively uncommon in most insect groups, but has been recorded for some tephritid flies (Diptera: Tephritidae) (Prichard 1969, Shelly 1999), water striders (Hemiptera: Gerridae) (Nummelin 1988), aphids (Hemiptera: Aphididae) (Inbar 1998), and webspinners (Embioptera) (Bradoo and Joseph 1970). Egg-brooding females of an African arachnophilic embiid viciously attacked experimentally-introduced conspecifics and at times succeeded in “plucking a leg or few antennal segments off the intruders” (Bradoo and Joseph 1970). Among the Hymenoptera, both ants (Formicidae) (Hölldobler and Wilson 1990) and parasitic wasps (Chalcidoidea) (Griffiths and Godfray 1988) often establish and defend foraging territories. Some parasitic wasps have been reported to defend a host resource, their eggs, or their offspring from conspecifics (Field and Calbert 1999, Hardy and Blackburn 1991, Wilson 1961).

Under field conditions, dispersing *Melittobia* females are temporally and spatially clumped, and usually crawl rather than fly to locate hosts (Freeman and Ittyeipe 1976). Potential hosts also may be clumped and persistent in favored locations. Thus, multiple parasitism is probably a rather common phenomenon. Molunby (1996), for example, found 1 to 5 (mean = 1.8) *M. femorata* females per host in midsummer *T. politum* nests in Mississippi. Some sort of response to such encounters would be warranted, and could be expected to differ for each species (and combination thereof).

Despite superficial similarities in host and lifestyle and overlapping geographic ranges, the behavior and life history of the four species in this study all differ from one another in significant ways; *M. femorata* in particular is not a typical member of its genus (Matthews et al. 2005, Matthews and González 2008). In addition to two distinctly separated non-overlapping adult generations on a single host, it shows striking differences in life history and morphology (Matthews and González 2008). Distinctly smaller than the other species, *M. australica* might be predicted to lose out in more interspecific battles, as in fact it did (Tables 2 and 3); interestingly, it also is the only species among those studied that does not belong to the *acasta* group of Dahms (1983a). The contrast between such an extreme degree of intraspecific female pugnacity in *M. femorata* and *M. acasta*, and its absence in *M. digitata* and *M. australica* was unexpected, particularly since *M. digitata*, *M. femorata*, and *M. acasta* are thought to be closely related and were placed in the same species group by Dahms (1984a) on the basis of morphology.

Why should females of *M. digitata* and *M. australica* tolerate conspecifics? Their communal oviposition is clearly facultative, since a single female has the ability to produce large numbers of eggs sufficient to fully consume the host upon hatching. Perhaps any disadvantages are outweighed by benefits accruing to larvae or the mixing of broods. Genetic studies could be enlightening.

One should not discount the possibility that the context in which we observe these interactions is not the same as the one in which the pugnacity

evolved. While mud-dauber wasps are commonly assumed to be the principal host of all these species, this could be simply a sampling bias brought on by the conspicuous nature of the highly visible, long-lasting nests. In addition, while today's high mud dauber nest densities provide a good likelihood that two or more female *Melittobia* emerging from the same clutch may jointly colonize a nearby host, this phenomenon may be relatively recent, an artifact of human activities such as bridge and barn building. Perhaps other solitary bees and wasps were the principal original hosts for the four *Melittobia* species, such that each species' fundamental behavioral ecology and selection pressures may have been very different from that carried over into the laboratory from mud dauber nests.

For *M. digitata* and *M. australica*, one laboratory study has compared progeny production of groups of one to five conspecific females given a single blowfly host (Silva-Torres and Matthews 2003). While absolute numbers from this smaller artificial host cannot be directly compared to our results, the relationships would be expected to be similar. In that study, as in ours, both alone and with up to five females of their own species, *M. digitata* produced more offspring than *M. australica* for every group size. Offspring of both species developed slightly faster when in competition than under sole foundress conditions.

Given that multiple foundresses of *M. femorata* readily attack one another on a new potential host, it is interesting to note that newly mated *M. femorata* females cooperate to chew a common exit hole (Deyrup and Matthews 2007a), just as *M. digitata* do (Deyrup et al. 2005). Comparing the behaviors of host feeding and cooperative escape-chewing in *M. digitata*, Deyrup and Matthews (2007b) found they were very similar, and suggested that the two behaviors have a similar biological basis. In *M. femorata* we have the seeming contradiction of a species in which cooperative chewing for escape and aggressive interactions coexist; it may be instructive that aggression only occurs when oviposition commences, days after host feeding has occurred.

While there appear to be no published papers on interspecific female competition in *Melittobia*, it most likely occurs in nature. As noted above, we have on occasion found females of 2 (and once, 3) species in a single mud dauber cocoon. This observation suggests that females' host-searching behavior must be somewhat flexible, and that both inter- and intraspecific host sharing does occur. Whether host sharing females can somehow assess a competitor's size and/or reproductive status and make conditional decisions about whether to stay or leave remains to be studied. Our laboratory experiments were admittedly artificial in that both females were simultaneously introduced to the host and had no opportunity to leave to search for another. In nature, two females would most likely arrive at different times, giving one a head start, and later arrivals would have a fight-or-flee option.

What selects for one species to behave aggressively, but not another? Genetic analysis of female relatedness, experimental manipulation of host searching cues and discovery context, and further life history research may ultimately lead to answers. Certainly one could hardly ask for a more amenable group than *Melittobia* with which to address that question; these four sympatric parasitoids are commonly found, easily reared, readily manipulated, and appear to display a continuum of aggressive interactions in both sexes, promising that such further study will be both agreeable and rewarding.

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