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Source: Florida Entomologist, 89(2) : 135-140

Published By: Florida Entomological Society

URL: [https://doi.org/10.1653/0015-4040\(2006\)89\[135:FASCIA\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2006)89[135:FASCIA]2.0.CO;2)

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FEEDING AND SIBLICIDAL CANNIBALISM IN A MALE PARASITIC WASP (HYMENOPTERA: EULOPHIDAE)

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ABSTRACT

Melittobia digitata Dahms is a small parasitic wasp known for its lethal male combat but subject to controversy regarding the occurrence of male feeding and cannibalistic feeding in particular. Here we report our observations supporting siblicidal cannibalism. To test the ability of a male's capability to feed we smeared sugary dye on the wasps' mouthparts and observed the dye passing through the digestive system to produce colored feces, confirming that males have a complete digestive tract. To document siblicidal feeding we injected other males with water-soluble dye, and paired them with undyed males. Undyed winners that appeared to feed on dyed losers were monitored; dye was evident in their feces. Finally, to determine if males benefit from feeding, we compared the longevity of artificially fed and unfed males; fed males lived significantly longer than non-fed males (Mann-Whitney U test = 81.5, $N_1 = 26$, $N_2 = 26$, $P < 0.001$). We discuss possible reasons for the comparative rarity of siblicidal cannibalism and its fitness implications.

Key Words: *Melittobia*, kin selection, uneven sex ratios, male combat

RESUMEN

Melittobia digitata Dahms es una avispa parasitoide conocida por sus combates letales entre machos pero que está sujeta a controversia respecto a la existencia de alimentación por estos en general, y canibalismo en lo particular. Se reportan aquí nuestros hallazgos en cuanto a canibalismo. Para probar la habilidad de un macho para comer se le untó una pasta azucarada coloreada en las partes bucales de la avispa. Se observó pasar a través del sistema digestivo para producir heces de color, confirmando así que los machos tienen un sistema digestivo completo. Para documentar canibalismo entre hermanos se inyectó a otros machos un colorante soluble en agua y se colocaron con machos normales. Se monitorearon los ganadores no coloreados parecieron alimentarse sobre los perdedores coloreados; el colorante era evidente en sus heces. Finalmente, se determinó el beneficio de alimentarse, comparando la longevidad de machos alimentados y no alimentados (artificialmente); los machos alimentados vivieron significativamente más tiempo que los no alimentados (Prueba U de Mann-Whitney = 81.5, $N_1 = 26$, $N_2 = 26$, $P < 0.001$). Discutimos razones posibles para la rareza del canibalismo entre hermanos y sus implicaciones adaptativas.

Melittobia (Hymenoptera: Eulophidae) are small, gregarious parasitoids of solitary wasps and bees, and assorted associates (Edwards & Pengelly 1966; Krombein 1967; Maeta & Yamane 1974). These parasitoids have intrigued biologists (e.g. Hamilton 1967) because of their unusual and highly inbred reproductive strategy. *Melittobia digitata* Dahms is also used in educational curricula under the name WOWBug® (Matthews et al. 1996, 1997).

Upon finding a suitable host, the female *Melittobia* stings it, feeds on hemolymph exuding from the sting wound, and then lays several hundred eggs, of which over 90% develop into females (Buckell 1928; Schmieder 1938; Dahms 1984). Females mate once with a brother, and then cooperate to chew an exit hole and disperse (Deyrup et al. 2005); their brothers remain behind to die within their natal host's cocoon (Dahms 1984).

While males' lives may be circumscribed within their natal cocoon, they are nonetheless action-filled. Males of most *Melittobia* species are highly pugnacious and frequently engage in fatal fights with their brothers (e.g., Graham-Smith 1919; Malyshev 1968; Matthews 1975; Hamilton 1979; Hartley & Matthews 2003; Abe et al. 2003); attacks on male pupae are also documented (Hermann 1971; Abe et al. 2005) and, because *Melittobia* are protandrous, male fighting can begin before the first females emerge. Occasionally, however, males also will attack females presented to them (Balfour-Browne 1922; Hermann 1971; Matthews 1975; Dahms 1984).

There has been speculation as to whether, in addition to the obvious advantage of dispatching potential rivals, such attacks might provide an opportunity for males to feed (Matthews 1975). Several biologists have gone on record as doubt-

ing that *Melittobia* males feed at all. For example, while Dahms (1984) observed attacks, he found no evidence of feeding and pointed out that a male's gaster grows increasingly thinner until he dies. Abe et al. (2005) categorically state that males of *M. australica* Girault do not feed. Balfour-Browne (1922) noted chewing attacks, but considered them to be an artifact of experimental conditions. Others disagree, reporting that males sometimes continue to chew on a defeated male sibling (Graham-Smith 1919; Matthews 1975) or on an attacked female (Hermann 1971) for relatively extended periods of time. If they were to ingest nutrients during this behavior, such canni-

balism might provide a competitive advantage (Matthews 1975), enabling a male to live longer or produce more sperm.

Combat between males of *Melittobia digitata* is particularly intense. We noticed that *M. digitata* males in our laboratory cultures sometimes spent an extended period of time with their mandibles immersed in the tissues and hemolymph of a defeated male (Fig. 1). In one instance, a male killed an emerging male by biting through the emerging male's head capsule, and then inserted his mandibles deeper into the head capsule. The victor's palpi were highly active, with motions resembling those of feeding females. As we watched,

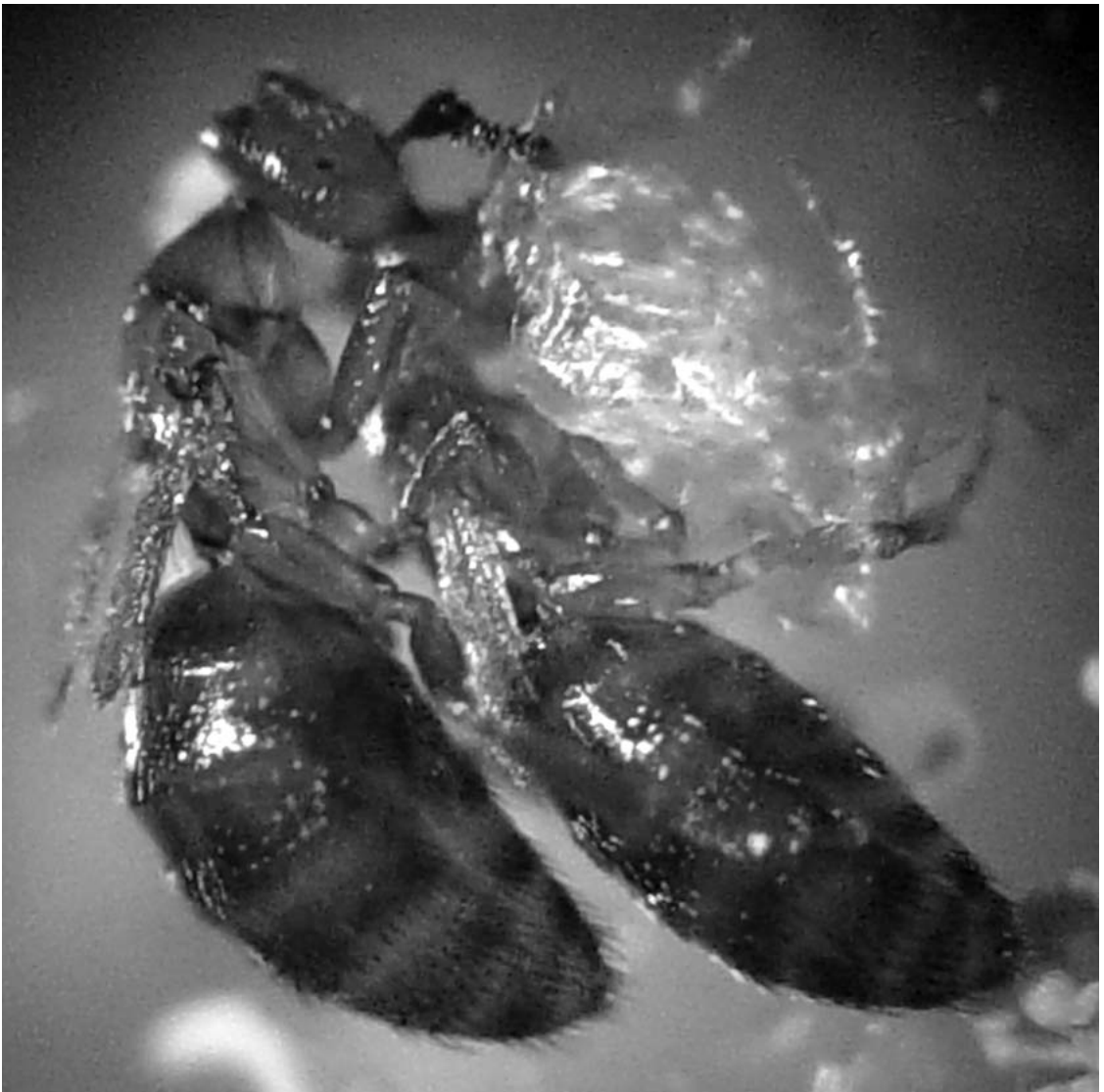


Fig. 1. A male of *Melittobia digitata* Dahms that appears to be feeding on a sibling male (Photo courtesy of Jorge M. González).

the abdomen of the male began to swell slightly, as if hemolymph were filling the crop. This observation lent support to a hypothesis that *M. digitata* males sometimes feed on a defeated male, and encouraged our experimental approach to male feeding with three objectives. The first was to determine whether male *M. digitata* have a functional digestive tract. The second was to resolve whether males ingest hemolymph from other males, and, if so, whether it passes through their digestive system. The last was to test whether individual males benefit from feeding.

MATERIALS AND METHODS

Experiment 1: Functional Digestive Tract

We collected 40 *M. digitata* male pupae (recognizable by the lack of compound eyes) developing in a single laboratory culture, isolated them individually in small tightly lidded plastic boxes (50 × 25 × 18 mm, Carolina Biological Supply Co., Cat. No. ER-14-4584), recorded eclosion dates, and randomly assigned the adults either to the control or experimental group. The controls were undisturbed. When wasps in the experimental group were 2 days old, we smeared their mouthparts with either “willow green”, “cornflower blue”, or “rose petal pink” cake icing dye (Wilton Enterprises).

After the passage of several hours to allow opportunity for treated males to groom, all males were transferred into clean boxes. We checked the boxes daily and recorded whether colored fecal droppings appeared. We also observed the males under a dissecting microscope to check for dye in their digestive system, and found that it was clearly visible through their translucent cuticle. A χ^2 test in was used to determine whether individuals in the experimental and control groups differed significantly in passing colored fecal spots vs. undyed spots (Statistica 6.0).

Experiment 2: Feeding on Another Male

Because we reasoned that nutritionally stressed males would be more likely to feed, we stressed males by isolating individual late male pupae (± 1 d until eclosion) and providing each with 10 newly eclosed virgin females. Males were allowed to mate *ad libitum* with these females for up to 5 days post-eclosion. After 3-5 days the males' gasters became thin and they appeared emaciated.

To produce weakened males with identifiable hemolymph as potential losers, we injected them in the abdomen with blue water-based dye (McCormick & Co., Inc.) using a glass pipette (Soda Lime Glass, 9", J. & H. Berge, Inc.) that had been stretched while heating it in an alcohol flame. Typically, the dyed male rapidly weakened, and was usually dead in 10 to 15 min.

An emaciated undyed male and a “weak” freshly dyed male were paired in a deep well projection slide arena (Carolina Biological Supply, Inc.). Because there was only a short window of opportunity for combat, we placed them next to each other to facilitate interaction; even then, most fighting was non-lethal. Even after lethal fights, most males did not attempt to feed on their defeated brother. However, we continued to dye, expose, and observe the males until we recorded 10 instances of undyed victors that killed their dyed brother and appeared to feed upon them. Each of these victors was placed into a separate observation box and observed for subsequent dye passage in its fecal droppings.

Experiment 3: Benefit from Feeding

To determine whether males benefit from feeding, we gathered 55 *M. digitata* male pupae from five cultures, isolated each pupa in a glass 1 dram vial, and inspected the vials daily, recording the date on which each male eclosed; 52 pupae eclosed as adults. Males that eclosed on the same day were assigned to an experimental (fed group, $n = 26$) or a control (unfed, $n = 26$) group.

The experimental group was fed insect hemolymph from a *Trypoxylon* (*Trypargilum*) *politum* Say prepupa. Using an insect pin to puncture the host prepupal cuticle, we bled one drop of hemolymph onto a glass slide then gently transferred a male to the drop with a fine brush. Males immediately imbibed hemolymph from the drop. When a male did not drink voluntarily, we coaxed its head into the drop. The males invariably fed when their mouthparts touched the hemolymph, and we allowed males to feed to satiation. The control group of males was not fed. We did not give them water or insect saline solution; such resources do not occur in their natural habitat, because males seldom, if ever, leave the pupa case of their host.

All individuals in both groups were individually isolated in 1-dram glass vials and placed in an incubator at 30°C. We recorded how many days each male survived. The difference between the treatment and the control groups was analyzed using a Mann-Whitney U test and a survival analysis (Statistica 6.0).

RESULTS

In the first experiment, all colors of dye were immediately visible passing through the upper digestive system into the crop of all 20 treated males, and color appeared in their droppings when checked 24 h later. Whereas all males leave at least some fecal specs, no control males ever had droppings of a color similar to those of the fed males. This difference was very highly significant using a χ^2 test ($\chi^2 = 40.0, P < 0.001$) (Statistica 6.0).

In experiment 2, each of the males that we had suspected of feeding on his brother had blue color moving through the body and into the crop. This was confirmed when we checked 24 h later that dye was passed in droppings of all 10 individuals.

In experiment 3, individual male adult life spans varied, ranging from 12-16 d for unfed males, and from 13-18 d for fed males (Fig. 2). However, the lives of fed males were 1.5 d longer, on average, than those of unfed males (unfed \pm SE = 13.2 ± 0.14 , $\bar{x} = 13$; fed \pm SE = 14.7 ± 0.21 , $\bar{x} = 15$). Statistically, the difference was very highly significant (Mann-Whitney U test = 81.5, $N_1 = 26$, $N_2 = 26$, $P < 0.001$) (Statistica 6.0).

DISCUSSION

The results from experiment 1, demonstrating that the digestive tract of male *M. digitata* is complete and apparently functional, led to the second experiment, which established that males that defeat another male are capable of ingesting hemolymph from the defeated individual. The combination of these two experiments supports the assumption that the apparent feeding behavior that we had previously observed was correctly interpreted because males of *M. digitata* have a functional digestive tract and are capable and will imbibe hemolymph from another male.

We showed that *M. digitata* can feed, but our findings may not apply to all species in the genus. For example, *M. femorata* Dahms does not appear to have the same propensity for lethal male combat as *M. digitata* (R. W. M., unpublished data). While an *M. femorata* male conceivably could feed on a killed female, it would be unlikely to feed on a brother.

Records of feeding by adult male parasitoids are rare. Males of few species have access to

hemolymph, and *M. digitata* seems to take an advantage of an unusual situation. Nectar is a more usual food source for adult Hymenoptera, but nectar-feeding by parasitoids is also rare, and concentrated in a few families. At the Archbold Biological Station (Highlands Co., FL), where flower visitors have been studied for many years, there are few records of nectar feeding by male parasitoids. Among Ichneumonoidea, nectar feeding occurs in male *Agathis longipalpus* (Cresson) (Braconidae); among Chalcidoidea nectar feeding occurs in male *Leucospis affinis* Say, *L. robertsoni* Crawford and *L. slossonae* Weld (Leucospidae). In contrast, male aculeate Hymenoptera are frequent nectar feeders at the Archbold Biological Station, including numerous species representing 15 families (M.A.D., unpublished data).

Reports of adult male siblicidal cannibalism in insects are relatively rare. A situation somewhat similar to that of *Melittobia* occurs in ants of the genus *Cardiocondyla*; ergatoid males engage in lethal combat, usually won by an older male that attacks a recently eclosed sibling (Stuart 1987; Heinze et al. 1998). In this genus, however, workers remove the dead male from the nest or feed it to larvae (Stuart 1987). The situation confronting *Melittobia* males differs from that of ants in that *Melittobia* males exist in a closed system, without access to external resources.

In mites, female cannibalism has been reported (Schausberger & Croft 2000; Berndt et al. 2003), but its possible siblicidal nature seems to require further study. Schausberger & Croft (2000) reported that *Phytoseiulus persimilis* Athias-Henriot preferentially cannibalized non-siblings, but later Schausberger (2003) reported that if raised without contact with siblings, they preferentially cannibalized siblings. *Melittobia digitata* males have been reported to occasionally kill female siblings but whether they also cannibalize them is not clear (González & Matthews 2005).

Cannibalism for its own sake would seem to have several potential disadvantages. The three most applicable to *M. digitata* males are the risk of being injured or killed in attacking a similarly capable individual, the risk of contracting a disease from the consumed individual, and the evolutionary cost to fitness (Elgar & Crespi 1992). However, like *M. digitata* attacking male pupae, some species seem to avoid the problem of attacking a similar organism when early maturing individuals or individuals of a more advanced developmental stage kill a less capable immature individual (Elgar & Crespi 1992). However, this is not always the case; for example, cannibalism on peers has been recorded in intrauterine sharks (Pours 1977; Hamlett & Hysell 1998). In *M. digitata* violent combat, presumably evolved in the context of local mate competition, usually quickly incapacitates the defeated male, thereby removing the risk of further injury. This would

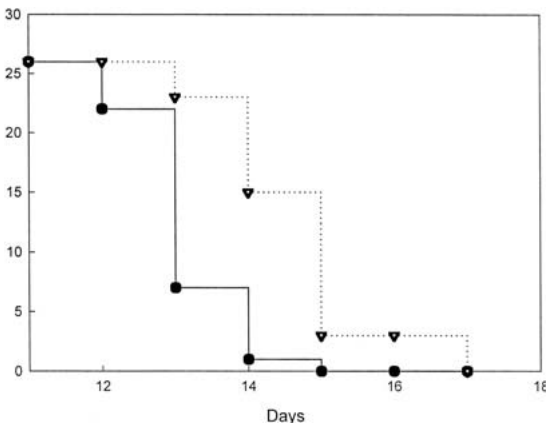


Fig. 2. Longevity of fed and unfed males of *M. digitata* at 30°C (dotted line and ▽ = males that were fed hemolymph; solid line and ● = males that were unfed).

leave victorious males free to consume the defeated male without further risk. Similarly, cannibalism among male *Melittobia digitata* seems unlikely to transmit disease, as the combatants are usually siblings, having fed off the same host, and lived their entire lives inside a sealed cocoon. The third potential disadvantage, loss of fitness in sibling competition, is a complex issue; kin selection models have endeavored to deal with this problem (Griffin & West 2002). However, cannibalism after combat adds yet another advantage in *M. digitata* male competition.

The third experiment showed that males who fed lived significantly longer than unfed controls. Lengthening one's adult life by the equivalent of 11% is no biologically trivial matter; presumably, those males that live longer secure more mates, dispatch more rivals, and have increased fitness relative to unfed males. Wiltz and Matthews (unpublished) found that males are more likely to die before exhausting their sperm, which makes longevity a better indicator of increased fitness than sperm production. We have observed males feeding on eclosing males and on pupae that are more vulnerable. Added longevity in males that emerge with the first generation of a few short wing females would benefit greatly in fitness by the extended overlap with the subsequently emerging group long wing females. Wiltz and Matthews (unpublished) study and our observations expose the possible benefits for males who can extend their lifespan by feeding.

We conclude that male cannibalism in *M. digitata* may not be rare when the advantages outweigh the disadvantages. The natural history of *M. digitata* appears to satisfy this criterion. The fact that a single male can potentially inseminate over 200 sisters and is likely to die before exhausting his sperm (B. Wiltz & R. Matthews, unpublished), as appears to occur routinely in some *Melittobia* species, provides a context in which male feeding and increasing life expectancy would be advantageous. Male *M. digitata* that defeat and then cannibalize brothers may also obtain nutrients needed to maintain sperm production and sex pheromone production (Consoli et al. 2002) for an extended life expectancy, as well as acquire the energy needed to successfully combat newly eclosing brothers (Abe et al. 2005) and repeatedly perform the relatively elaborate courtship displays that characterize the genus (Matthews & Matthews 2003, González & Matthews 2005).

ACKNOWLEDGMENTS

We thank and appreciate Jan Matthews and Jessica Beck for reviewing the manuscript, Jorge M. González for the photograph and stimulating discussion, and Stuart West for his knowledge and insightful ideas. This project was supported by an NSF grant (R. W. Matthews, P.I.).

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