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# FEMALE AND MALE POLYMORPHISM IN TWO SPECIES OF *MELITTOBIA* PARASITOID WASPS (HYMENOPTERA: EULOPHIDAE)

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ABSTRACT

Polymorphism appears to be fundamental in *Melittobia* wasps, but uncertainty exists as to its extent and form. Most researchers recognize 2 basic female forms—a long-winged dispersive "type form" and an early-maturing, short-winged gravid "second form." However, some investigators have recognized two macropterous forms, "jumpers" and "flyers." Many others have suggested that males, which normally comprise only about 5% of the population, also may exist in 2 forms in various *Melittobia* species. This study examined the role of maturational factors in 2 widespread representatives of different species groups, *M. australica* (*hawaiiensis* group) and *M. digitata* (*acasta* group). Individuals of both sexes from different points in the emergence curve were examined and measured immediately after eclosion and 5 d later. Both sets of measurements supported the existence of 2 clearly defined female morphs. However, when newly eclosed macropterous females were randomly assigned to 5-d placements in empty vials or with prepupal hosts (*Trypoxylon politum* Say), subsequent tests in a flight arena demonstrated that "jumpers" and "flyers" were simple reflections of macropterous female physiological state, with heavier, gravid females reluctant to do more than a slow crawl, and lighter, more nutritionally stressed females being more inclined to fly. Thus we conclude that there is no justification for recognizing a "jumper" morph. Male morphometrics indicated continuous variability in size and pigmentation of simple eyes and ocelli, but no morphologically distinctive male morphs at any point in the emergence curve. However, reports of distinct male morphs in other *Melittobia* species cannot be dismissed.

Key Words: brachyptery, morphometrics, flight, hopping, locomotion, eclosion order

RESUMEN

El polimorfismo parece ser fundamental en avispas del género *Melittobia*, aunque no existe certeza de su forma y extensión. Muchos investigadores reconocen dos formas femeninas básicas—una dispersiva, con alas largas, la "forma típica", y una de maduración temprana, las grávidas "forma secundarias" de alas cortas. Sin embargo, algunos investigadores han reconocido dos formas macrópteras, "saltadoras" y "voladoras". Otros han sugerido que entre machos, los cuales conforman cerca del 5% de la población, pueden existir también dos formas en varias especies de *Melittobia*. Este estudio examina el papel que cumplen los factores de maduración en dos representantes ampliamente distribuidos de dos grupos, *M. australica* (grupo *hawaiiensis*) y *M. digitata* (grupo *acasta*). Se examinaron individuos de ambos sexos de diversos puntos en la curva de emergencia, midiéndolos al eclosionar y luego de cinco 5 días. Ambos juegos de medidas apoyan la existencia de dos formas femeninas. Sin embargo, cuando a hembras macrópteras recientemente eclosionadas se colocaron al azar a los 5 días en contenedores vacíos o con prepupas de sus hospedadoras (*Trypoxylon politum* Say), pruebas subsecuentes en una arena de vuelo demostraron que las supuestas formas "saltadoras" y "voladoras" son solo el reflejo del estado fisiológico de las hembras macrópteras, en las cuales las grávidas, mas pesadas, son reacias a hacer algo diferente a caminar, mientras que las más ligeras, estresadas nutricionalmente, están mas dispuestas a volar. Es así como concluimos que no existe justificación para reconocer una forma "saltadora". La morfometría entre machos indica que existe una variabilidad continua en tamaño y pigmentación de ojos y ocelos, pero no necesariamente existen formas masculinas distintas en cualquier punto en la curva de emergencia. Sin embargo, reportes sobre formas distintas en machos de otra especie de *Melittobia* no pueden ser descartados.

Translation provided by the authors.

Polymorphism is extensive in the wasp genus *Melittobia* (Hymenoptera: Eulophidae). Males and females of these small, arrhenotokous, gregariously developing parasitoids differ from each other in color, wing size, eye structure, and gross morphology. In addition, researchers have repeatedly noted that each sex also seems to exhibit more than one morphological form (Assem & Ma-

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eta 1980; Dahms 1984; Freeman & Ittyeipe 1982; Schmieder 1933).

The most visibly prominent element of female *Melittobia* polymorphism is wing length. Wing polymorphism is widespread in insects, with determinants that can be genetic, environmental, or both. Its significance relates to dispersal, and the phenomenon usually involves tradeoffs between flight capability and ovarian investment (see review in Zera & Denno 1997). The first to describe this in *Melittobia* was Schmieder (1933), who discerned 2 female forms in *M. chalybii,* labeling them as the "type form" and "second form" based on wing development. Some 40 years later, Freeman & Ittyeipe (1976, 1982) identified 3 female morphs in *M.* sp. (*hawaiiensis* group), which are now considered to be *M. australica*. Their brachypterous "crawlers" were clearly equivalent to Schmeider's "second form", but within the macropterous, positively phototactic group, they distinguished 2 forms that differed in their propensity for flight. One form, the "jumpers", had slightly swollen abdomens and wing tips that did not extend beyond the abdomen tip; the other form, the "flyers," had more slender abdomens, and their wings extended beyond the tip of their abdomens. The 2 researchers suggested that this female trimorphism was an adaptation to exploit 3 spatial levels of host distribution (Freeman & Ittyeipe 1982).

Meanwhile, studies were suggesting that male *Melittobia* also might be polymorphic. Early studies of *M. chalybii* by Schmeider (1933, 1938, 1939) and his collaborators (Schmieder & Whiting 1947; Whiting 1947; Whiting & Blauch 1948) were joined by observations of Freeman & Ittyeipe (1982) on *M. australica.* In both of these species, researchers noted that some males seemed to be larger and had pigmented eyespots and ocelli, whereas other males were smaller and did not have pigmented eyespots and ocelli. There also were tantalizing signs that male *Melittobia* of various other species might exhibit 2 forms (Assem & Maeta 1980; Hartley & Matthews 2003; Lapp 1994).

But how many of these polymorphic forms actually exist as distinct entities? Rearing various species of *Melittobia* in our laboratory, we had questions. While we could easily discern 2 female forms—a long-winged, positively phototactic disperser and a short-winged non-disperser—we could not reliably distinguish between jumpers and flyers. Moreover, males (which comprise only 5% of most populations) are pugilistic and even cannibalistic toward one another, and most commonly are observed only after they have died; our observations of dead males showed considerable morphological variation, which might or might not be attributable to such factors as male age or desiccation. Furthermore, the majority of published observations suggesting male polymorphism had been based on the catch-all group, *M. chalybii*; knowing that this designation has been applied to at least 4 different species (Gonzalez & Matthews 2002), we thought it plausible that males identified as different morphs might even have been males of different species.

Therefore, the objectives of this study were to quantify differences purported to distinguish *Melittobia* morphs, and to clarify the role of various life factors in the expression of behavior and morphology within each sex of *Melittobia*. To do so, we undertook morphometric and behavioral examinations of individuals of 2 common North American species, *M. digitata* Dahms and *M. australica* (Girault), comparing females reared identically except for feeding regimen before being placed in a flight test arena, and comparing identically reared males grouped by emergence sequence. Our hypotheses were that apparent male polymorphism and apparent female macropterous subgroup polymorphisms were artifacts of natural male size variation and female nutritional condition, respectively.

## Materials and Methods

### Rearing Protocol

Each culture of *M. australica* or *M. digitata* was initiated by placing 1 mated female upon a naked prepupa of *Trypoxylon politum* Say (Hymenoptera: Crabronidae) within a shell vial maintained at 25°C under constant darkness. After 18 d, males and females were separated as late pupae, at which time the sexes can readily be established. Eclosion occurs over a week or more in these species. Each day, as new adults of both sexes appeared, they were removed and slide-mounted for morphology measurements. Females from identically reared cultures were removed and maintained for behavioral studies as outlined below.

### Morphological Measurements

Using an ocular micrometer, we measured wing length, hind tibia length, and abdomen length of each individual. Also for males we measured head width and recorded the occurrence of pigmentation in their simple eyes (eyespots) and ocelli. To assess whether male morphometrics or pigmentation patterns were related to development or emergence schedule, we partitioned male data into 3 age categories—early (d 1-3), middle (d 4-7), and late (d 8-11)—based on a previous study chronicling emergence patterns (Adams 2002).

### Behavioral Studies

Additional cultures of each species, reared identically, were used to further assess macropterous female locomotory behavior and test

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the hypothesis that macropterous "jump vs. flight" propensity might be due to fluid/food ingestion rather than being a genetically determined proclivity.

A simple flight arena was constructed by standing a round wooden toothpick (25 mm long) on a platform in the center of a white poster board marked with concentric rings at 50, 100, and 150 mm. Pilot tests confirmed that a female wasp released at the base of the pick and prodded gently with the bristles of a small camel's hair brush would almost invariably respond by climbing to the top of the pick. From here she had the choice of flying off, jumping off, turning around and climbing back down, or simply becoming a polesitter. Pilot trials showed that the overwhelming majority of newly eclosed females of both species preferred the latter 2 options, but flight and jumping both occurred regularly in these populations. The longest jumping distance recorded was less than 100 mm.

Within 1 d of eclosion from our experimental cultures, females were tested individually with this system. Once on the pick, the wasp was allowed up to 5 min to either launch herself into the air, crawl down and off, or remain on the pick. If genetically determined sub-morph differentiation into "jumpers" and "flyers" were present within this macropterous population, it should manifest itself most clearly in the behavior of those individuals that chose to launch themselves off the pole at this early stage of their adult lives. Thus, individuals that crawled down and off the pick or were still crawling on the pick after 5 min were disregarded. Those that launched from the pick were assigned to 4 distance-based groups until the sample size of each group reached at least 20 individuals. As determined by landings within the concentric rings on the flight arena floor, launches were scored as less than 50 mm, 51-100 mm, 101-150 mm, and more than 150 mm.

Females landing less than 50 mm from the pick were considered equivocal and were excluded from further study; these wasps may have fallen off the pick, jumped, or possibly flown in a tight loop. At the other extreme, females that covered distances of more than 150 mm in the arena clearly had flown, and thus were considered to be equivalent to the "flyers" of Freeman & Ittyeipe (1982). Because the pilot study indicated that jump distance never exceeded100 mm, those covering 101-150 mm most probably were all flyers, but to reduce uncertainty we excluded them as well. Only wasps that went 51-100 mm were considered equivalent to Freeman & Ittyeipe's "jumpers."

Those "flyers" and "jumpers" meeting the above criteria then were randomly assigned to one of 2 nutritional subgroups. Individuals in 1 subgroup ("fed") were provided with a *T. politum* prepupa; individuals of the other subgroup ("unfed") were placed in an identical empty container. After 5 d, all females were again individually tested in the flight arena by the same protocol, and their abdomen lengths were again measured. Video recordings were made of selected individuals' performances in the flight test arena to assist in discerning specific behaviors related to flight and jumping.

## Results

### Male Morphometrics

In all, the wing lengths, hind tibia lengths, and head widths of 52 freshly eclosed males of *M. australica* and 133 freshly eclosed males of *M. digitata* were measured, and ratios of hind tibia:wing length and hind tibia: head width were calculated (Table 1).

In both species, when measurements taken upon the first and last group of males to emerge were compared, clear differences in both wing length and head width were apparent. However, when the middle group was included, a continuous size variation and loss of a bimodal size distribution resulted (Table 1).

Ratios of the hind tibia length to wing length or head width revealed no consistent differences relating to emergence time. However, wing lengths of the first few *M. digitata* males to eclose were

Table 1. Variation in male size and form for *M. australica* and *M. digitata* by eclosion sequence.

| Eclosion interval (d) | Forewing length (mm) | Hind tibia length (mm) | Head width (mm) | Hind tibia/wing | Hind tibia/head width |
|---|---|---|---|---|---|
| *M. australica* ($n$ = 15 per eclosion interval; 45 total) | | | | | |
| 1-3 | 0.49 ± 0.005 | 0.29 ± 0.005 | 0.39 ± 0.01 | 0.60 ± 0.007 | 0.75 ± 0.03 |
| 4-7 | 0.43 ± 0.02 | 0.28 ± 0.01 | 0.34 ± 0.02 | 0.62 ± 0.06 | 0.83 ± 0.05 |
| 8-11 | 0.39 ± 0.005 | 0.29 ± 0.005 | 0.30 ± 0.01 | 0.67 ± 0.04 | 0.89 ± 0.08 |
| *M. digitata* ($n$ = 21 per eclosion interval; 63 total) | | | | | |
| 1-3 | 0.50 ± 0.005 | 0.30 ± 0.01 | 0.40 ± 0.01 | 0.61 ± 0.02 | 0.76 ± 0.02 |
| 4-7 | 0.45 ± 0.02 | 0.30 ± 0.009 | 0.39 ± 0.009 | 0.65 ± 0.02 | 0.75 ± 0.02 |
| 8-11 | 0.43 ± 0.03 | 0.28 ± 0.01 | 0.37 ± 0.02 | 0.66 ± 0.04 | 0.76 ± 0.05 |

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significantly different from their later-eclosing brothers (Kruskal-Wallis Test, $P < 0.05$).

Males of *Melittobia* lack compound eyes, but have undeveloped simple eyespots and ocelli, and differences in their extent of pigmentation also have been suggested to signal the existence of 2 male morphs. Our analysis (Table 2) showed that overall pigmentation of both structures was the commonest condition, and that while variation did occur, there was no consistent pattern of pigment presence or absence in relation to emergence time. However, almost half (40%) of our sample exhibited variation in eyespot and/or ocelli presence and pigmentation. Unpigmented eyespots were invariably correlated with unpigmented ocelli, but 13/42 (31%) of the males with pigmented eyespots lacked pigmented ocelli.

### Female Morphometrics

Samples of 100 females of *M. australica* and *M. digitata* representing different developmental stages of the cultures were measured and compared (Table 3). Both species exhibited a clearly bimodal distribution of measures assignable to 2 morphological groups most obviously separated by wing length. In each species, the wing lengths of the 2 morphs could be clearly distinguished and were statistically significantly different from each other. Likewise, the ratio of hind tibia length to wing length clearly showed that females of each species exhibit only 2 clear morphs.

Absolute body sizes varied, but females of *M. digitata* were slightly larger than *M. australica* overall. Wings of brachypterous *M. digitata* females were more uniform in size than those of brachypterous *M. australica*. Variations in abdomen length (a highly variable character) and in abdomen: hind tibia length ratio were both continuous, thus also providing no support for the hypothesis of 2 distinct long-winged female morphs in the 2 species we studied.

### Behavioral Studies

Even with the naked eye, it is apparent that macropterous females of both species mostly walk about, but occasionally will hop and/or take short flights as well as rarer long ones (Matthews et al. 1996). Videotape recordings of females crawling about on toothpick towers revealed that the females often repeatedly raised the anterior part of their body and rapidly flexed their wings 1 or more times in a few seconds, inducing a contraction of the thorax. These behaviors typically preceded a launch from the pick and we consider them to be intention movements. Whether females also simply jumped off or dropped from the picks without accompanying wing flips was not confirmed, but probably also occurred.

At 1 d of adult age, most newly emerged long-winged females simply crawled and showed no strong tendency to launch from the toothpick, although flight >150 mm was observed.

All females provided with a host for 5 d became physogastric due to host feeding and consequent ovarian development. This state was easily observable, as the tips of their swollen abdomens now extended beyond the wing tips (Fig. 1). In contrast, long-winged females placed in empty containers for 5 d became more slender as their internal reserves were depleted; in consequence, their abdomens visibly shrunk so that their wing tips clearly extended beyond the tip of abdomen (Fig. 1).

Confronted with a second time atop the pole in the flight arena (Table 4), 5-d-old physogastric females displayed an extremely low propensity to launch themselves in any manner. (For example,

TABLE 2. EYESPOT AND OCELLAR PIGMENTATION IN MALES OF *MELITTOBIA AUSTRALICA* AND *M. DIGITATA* IN RELATION TO ECLOSION ORDER.

| Eclosion interval | Eyespots fully pigmented | | | No pigmented eyespot or ocelli[1] |
|---|---|---|---|---|
| | All ocelli fully pigmented | No ocellar pigmentation | Mixed ocellar pigmentation | |
| *M. australica* ($n$ = 45) | | | | |
| Early (d 1-3) | 8 | 5 | 1 | 1 |
| Middle (d 4-7) | 10 | 3 | 1 | 1 |
| Late (d 8-11) | 9 | 5 | 0 | 1 |
| All males | 27 (60%) | 13 (29%) | 2 (4.5%) | 3 (6.5%) |
| *M. digitata* ($n$ = 64) | | | | |
| Early | 12 | 4 | 2 | 3 |
| Middle | 10 | 7 | 2 | 2 |
| Late | 12 | 8 | 1 | 1 |
| All males | 34 (53%) | 19 (30%) | 5 (8%) | 6 (9%) |

[1]In both species, no individuals that lacked eyespot pigmentation were observed to have ocellar pigmentation.

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TABLE 3. FEMALE MORPH DIFFERENCES IN *MELITTOBIA AUSTRALICA* AND *M. DIGITATA*.

| Morph | Forewing length (mm) | Hind tibia length (mm) | Abdomen length (mm) | Hind tibia/wing length | Hind tibia/ abdomen length |
|---|---|---|---|---|---|
| *M. australica* ($n$ = 100) | | | | | |
| Long winged | 0.61 ± 0.08 | 0.29 ± 0.004 | 1.14 ± 0.13 | 0.49 ± 0.07 | 0.26 ± 0.02 |
| Short winged | 0.84 ± 0.09 | 0.30 ± 0.004 | 1.04 ± 0.06 | 0.35 ± 0.03 | 0.28 ± 0.01 |
| *M. digitata* ($n$ = 100) | | | | | |
| Long winged | 0.65 ± 0.10 | 0.30 ± 0.01 | 1.03 ± 0.05 | 0.47 ± 0.06 | 0.29 ± 0.01 |
| Short winged | 1.09 ± 0.06 | 0.34 ± 0.01 | 1.18 ± 0.06 | 0.31 ± 0.01 | 0.28 ± 0.01 |

in the earlier pilot study, only 1 of 12 *M. australica* and 0 of 18 *M. digitata* left the pole.) When they did launch themselves, few became airborne—only 15% of fed *M. australica* launchers flew, whereas 60% of the unfed launchers flew. For *M. digitata*, the differences were even more dramatic; none of the fed launchers flew, but 86% of the unfed launchers did.

## DISCUSSION

### How Many Female Morphs Does *Melittobia* Have?

Our data confirmed the existence of only 2 clearly defined morphological forms, brachypterous and macropterous, in both *M. australica* and *M. digitata*. These results concur with previous findings in other species (e.g., Schmieder 1933; Lith 1955; González 1994; González et al.1996; Lapp 1994). Recent work confirms that these morphs are nutritionally determined (Cônsoli & Vinson 2002). The first several offspring on a singly parasitized large host become brachypterous females that develop several days faster than their macropterous siblings, apparently due to better food quality, an assumption made originally by Schmieder (1933) and supported by Freeman & Ittyeipe (1982). However, if 2 or more *Melittobia* females superparasitize a host, few or often no brachypterous females are produced (unpublished observations), and only macropterous females result. In any case, the number of brachypterous females rarely exceeds 40 individuals, and is usually closer to 20 (Freeman & Ittyeipe 1982).

Although most behavioral studies of *Melittobia* have concentrated solely upon the long-winged form, it is clear that once set in motion, developmental and morphological differences play out in different behaviors throughout the lives of the 2 morphs. For example, the 2 morphs of *M. digitata*



Fig. 1. Grossly apparent differences in *Melittobia digitata* after 5 d of feeding upon a natural *Trypoxylon politum* prepupal host. (Left) The abdomen of fed females swells with ovarian development so that it extends beyond the wing tips. (Right) Unfed 5-d-old females have shrunken abdomens, such that the tips of the forewings extend beyond the abdomen tip.

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TABLE 4. LAUNCHING BEHAVIOR OF MACROPTEROUS 5-D-OLD *MELITTOBIA* FEMALES IN RELATION TO HOST-FEEDING STATUS.

| | Behavior inferred through landing distance from pick | |
|---|---|---|
| Nutritional status | "Jump" (51-100 mm) | "Flight" (>150 mm) |
| *M. australica* | | |
| Fed ($n$ = 20) | 17 (85%) | 3 (15%) |
| Unfed ($n$ = 37) | 15 (40%) | 22 (60%) |
| *M. digitata* | | |
| Fed ($n$ = 10) | 10 (100%) | 0 |
| Unfed ($n$ = 22) | 3 (14%) | 19 (86%) |

vary in courtship details (González & Matthews 2005). Ability to become airborne appears to be simply one more difference, in this case apparently reflecting body weight. As gravid, fed females of *M. australica* and *M. digitata* become "heavier", they show a reduced propensity to fly. On the other hand, in the absence of feeding, nutrient reserves diminish and the wasp becomes noticeably more slender, displaying a correspondingly greater tendency to fly. Thus, Freeman & Ittyeipe's (1976, 1982) findings probably simply reflected the confounding influence of food intake.

Freeman & Ittyeipe (1982) indicate that their jumper morph comprised only about 20-40 individuals intermediate in morphology to crawlers and flyers. However, they acknowledged that their 3 morphs overlapped in their morphologies, and recognized them primarily as "functionally distinct". In our experience, females use crawling as their primary form of locomotion, and undisturbed females rarely hop or jump spontaneously. However, jumping can be readily elicited if one "threatens" a female, e.g. with the tip of a pencil or paint brush (Matthews et al. 1996). Jumping thus appears to be primarily a predator avoidance response and, contrary to Freeman & Ittyeipe's assertion, seems unlikely to be used as a principal dispersal mechanism, The lack of unique morphological attributes further weakens the case for recognizing a distinct jumper morph.

Because host feeding induces ovarian development, a cascade of physiological and behavioral changes inevitably follows this act. However, ovarian development normally occurs only after successful dispersal and consequent host location; because gravid females do not usually leave their host, they would not be likely to engage in further extensive locomotion.

Whether these changes in locomotion should be attributed to feeding *per se* or to ovarian development is still an open question. It is worth remembering that host feeding is not the only source of food available to *Melittobia*; females readily ingest carbohydrates in the laboratory (unpubl. observ.) and may obtain honeydew and possibly floral nectar during dispersal. Ageing no doubt also affects behavior and physiology. Further work will be required to tease apart the roles of such factors as they affect dispersal and locomotion behavior.

What adaptive significance might there be in this little parasite's female polymorphism? As suggested for other examples of polymorphism in insects, the brachypterous morph may provide a trade-off of rapid fecundity against being flightless (Harrison 1980; Roff 1986; Tanaka 1993; Wheeler 1995). According to Cônsoli & Vinson (2002a) brachypterous *M. digitata* females emerge with a load of about 30 developed eggs, and following mating, start immediately laying them on their natal host. Although Freeman & Ittyeipe (1982) suggest that brachypterous females may disperse short distances, we have seen no evidence that they ever leave their natal host. Rather, they stay to further exploit their partially consumed natal host and thus fully realize their fecundity.

Simultaneously, it is obvious that total investiture in a non-dispersing morph would be a dead-end route, both in the short term and evolutionarily. The long-winged, powerfully jawed, and strongly phototactic females of the macropterous form are true dispersal machines. To compensate for their very small chances of successfully locating a new host, estimated by Freeman & Ittyeipe (1982) as a probability of 1 in 485, these females have much higher potential fecundity. We have recorded over 800 offspring on a single host for some *Melittobia* species (unpubl. observ.). Together, the 2 female morphs provide *Melittobia* with a strategy in which the whole could truly be said to be greater than the sum of its parts.

### How Many Male Morphs Are There?

Though some authors have postulated the existence of 2 male morphs in various species of *Melittobia*, data from our study fail to support the existence of 2 clear morphs in males in *M. australica* and *M. digitata*, and instead suggest that a continuum of morphological variation exists. For

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*M. australica*, this supports data in González et al. (1996). Behavior-based male morphs in *M. australica* also seem unlikely. Whereas Freeman & Ittyeipe (1982) postulated 2 morphological forms of males in *M.* sp. (*hawaiiensis* complex) (=*M. australica*), they acknowledged that they "saw no difference in the behavior of male morphs".

The early work of Schmieder (1933, 1938, 1939) and collaborators (Schmieder & Whiting 1947; Whiting 1947; Whiting & Blauch 1948) with *M. chalybii* has formed the basis for much of the speculation about male morphs in *Melittobia*, but is problematical because we now know that those researchers were actually working with up to 4 different species (González & Matthews 2002). Thus, the possibility cannot be discounted that males of 2 different species were considered as 2 different morphs of a single species.

Freeman & Ittyeipe (1982) reported that *M. australica* males in large broods (>40 adults) were more fully pigmented overall (including fully pigmented eyespots and ocelli) in comparison to more lightly pigmented "second form" males with "underdeveloped ocelli" that appeared only in small broods (up to 30 adults per standard host). Interestingly, Schmeider (1933) recognized a type form male with pigmented eyespots and ocelli but apparently his second "totally blind" form was darker, not lighter, than his type form. Our data indicated a great deal of variation in eyespots and ocelli, and failed to show an association between this variation and eclosion sequence. It is also worth noting that the *M. australica* males in our study were reared in very large broods (ca. 400 adults) that should have led solely to "type form" development by Freeman & Ittyeipe's (1982) criterion. Instead, we found pigmentation variants representing both supposed morphs and a range between.

*Melittobia digitata* is perhaps the most thoroughly studied of all the species in this genus. Most of the published research has centered upon the long-winged females. However, important studies by Cônsoli and his collaborators (Cônsoli & Vinson 2002a, b; 2004; Cônsoli et al. 2004) have confirmed that the brachypterous and macropterous female morphs are real, and are determined by host quality and quantity. The question as to whether this species also produces distinct male morphs by similar or analogous means has yet to be addressed. Certainly the present study found only continuous variation over time, as males became progressively smaller in absolute size but kept their basic same body proportions. However, it is worth remembering that our study addressed a male population all produced under one standard scenario; different rearing regimens might yield different results.

We also cannot discount the possibility of male morphs in some other *Melittobia* species. Assem & Maeta (1980) reported 2 distinct morphs in males of a *Melittobia* species from Japan (=*M. sosui*) and suggested that this dimorphism was not related to food supply. Working with *M. femorata* Dahms, Lapp (1994) distinguished 2 possible male morphs based upon their eclosion before and after the extended prepupal diapause that is apparently unique to this species (see Matthews et al. 2005). In a forthcoming study (Matthews & Gonzalez, unpubl. data), we present evidence that the first few *M. femorata* males from the pre-diapause clutch do consistently differ morphologically from those in the post-diapause, late-developing group.

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