BIOLOGICAL CONTROL

Development of *Melittobia australica* Girault and *M. digitata* Dahms (Parker) (Hymenoptera: Eulophidae) Parasitizing *Neobellieria bullata* (Parker) (Diptera: Sarcophagidae) Puparia

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Desenvolvimento de *Melittobia australica* Girault e *M. digitata* Dahms (Hymenoptera: Eulophidae) Parasitando Pupários de *Neobellieria bullata* (Parker) (Diptera: Sarcophagidae)

RESUMO - O desenvolvimento de *Melittobia australica* Girault e *M. digitata* Dahms parasitando pupários de *Neobellieria* (=*Sarcophaga*) *bullata* (Parker) foram estudados com densidades de um a cinco parasitóides fêmeas por pupário. Aspectos da biologia dos parasitóides tais como: número de descendentes produzidos, longevidade, e tamanho do corpo dos descendentes, podem ser afetados em função do número de parasitoides por pupário. Em geral, a porcentagem de pupários parasitados foi maior para *M. digitata* do que para *M. australica*. Independentemente da densidade de parasitóides por pupário, o número total de descendentes produzidos foi significativamente maior para *M. digitata* (66,5 a 158,0) que para *M. australica* (10,9 a 55,5). Para ambas espécies, o número de descendentes produzidos por fêmea dos parasitóides foi inversamente proporcional à densidade dos parasitóides. O aumento da densidade dos parasitóides prolongou o tempo de desenvolvimento *M. australica*, e ocasionou redução em *M. digitata*. A longevidade dos adultos emergidos de *M. australica* e *M. digitata* foi maior quando oriundos das densidades até três parasitóides por pupário, e o tamanho do corpo dos decendentes, mostrou significante redução quando aumentou a densidade de fêmeas dos parasitóides por pupário. Entretanto, a razão sexual dos descendentes não foi afetada, variando de 0,95 a 0,98 para *M. australica*, e de 0,95 a 0,97 para *M. digitata.* Os resultados mostram que *M. digitata* apresentou melhor desempenho que *M. australica* parasitando *N. bullata*, e ambas espécies apresentaram redução no desempenho aumentando a densidade de parasitoides por hospedeiro, sugerindo haver competição entre os descendentes.

PALAVRAS-CHAVE: Insecta, parasitóide, hospedeiro alternativo, razão sexual, plasticidade do desenvolvimento

ABSTRACT - The development of *Melittobia australica* Girault and *M. digitata* Dahms were studied parasitizing blow fly puparia *Neobellieria* (=*Sarcophaga*) *bullata* (Parker) using from one to five foundress females per host. Aspects of parasitoids biology such as number of descendents produced, longevity, and progeny body size can be affected as the number of foundress increases per host. The percentage of puparia parasitized was higher overall for *M. digitata* than for *M. australica*. Regardless of foundress numbers, the average total number of descendents produced was significantly higher for *M. digitata* (66.5 – 158.0) than for *M. australica* (10.9 – 55.5). The number of descendents produced per female was inversely proportional to the number of foundresses on a host for both species. Developmental time increased for *M. australica* and decreased for *M. digitata*, as the number of foundresses increased. Life spans of adult progeny of both species, deprived of host and food, were longer for progeny derived from fewer foundresses. Body size as measured by forewing and hind-tibia lengths of descendents showed significant reduction as number of foundresses increased for both species, except for the forewing of *M. digitata*. Changing foundress number did not affect offspring sex ratios (0.95 – 0.98 for *M. australica*, and 0.95 – 0.97 for *M. digitata).* These results indicated that *M. digitata* achieved better performance parasitizing *N. bullata* compared to *M. australica*, and both parasitoid species had their performance affected by increasing the parasitoid densities per host, suggesting that progeny competition occurred.

KEY WORDS: Insecta, parasitoid, facultative host, sex ratio, developmental plasticity

Members of the genus *Melittobia* are small, cosmopolitan, gregarious ectoparasitoids, which primarily attack solitary wasps, bees, and their inquilines (Freeman & Ittyeipe 1982, González & Terán 1996). A single fertilized female of *Melittobia* may produce several hundreds offspring from a suitable host, and these usually exhibit a highly skewed sex ratio, with about 95% females (Assem *et al*. 1982).

In all stages of development, *Melittobia* show remarkable plasticity of behavior and adaptability to prevailing conditions. Theoretically, even uninseminated females can survive and eventually produce progeny of both sexes, also in the absence of preferred hosts (Dahms 1984). In laboratory they accept a variety of hosts, including species of Diptera and Coleoptera (Thompson & Parker 1927). In nature, this seeming catholicity of tastes probably serves *Melittobia* well, in that it can reproduce both on the preferred host and upon the many other predators and parasites that commonly infest a mud dauber's nest (Matthews 1997a). The qualitative and quantitative relationships that exist between the population of a host insect and that of its parasitoid are of interest to ecologists and economic entomologists alike. Theoretically, many aspects of its usual biology might be affected. Changes might be observed in oviposition rate, offspring mortality, sex ratio, body size and fecundity. It is by such characters that we usually measure the "success" of a parasitoid.

According to Vinson (1988), the success of parasitism involves two major processes: host localization and recognition. Parasitoid females may choose a suitable host for their progeny's development as a result of preimaginal conditioning that sustains the localization and recognition processes. However, once a host is selected, a parasitoid female's reproductive success depends on her offspring's ability to fit their growth and maturation to the available host nourishment. However, artificial rearing under laboratory conditions is similar to a scarcity-of-hosts situation and in this scenario, females must decide between progeny production and egg retention. In laboratory experiments with various species of parasitoids under different constraints, researchers have found high variance in progeny production, a reduction in the number of descendents produced, alterations in body size and form, and variation in the offspring sex ratio (Freeman & Ittyeipe 1982, Godfray 1994, Ueno 1999).

At the same time, a second sort of scarcity-of-hosts situation can also occur, with many of the same theoretically possible results. This results from the fact that *Melittobia* emerge from their natal hosts in large numbers, and begin searching their immediate surroundings for new hosts upon which to lay their eggs. Many *Melittobia* hosts, including the mud dauber wasps, tend to have a highly clumped distribution (Cross *et al*. 1975, Molumby 1995) even though they are commonly called "solitary", because the adults do not form cooperative colonies. As a result, the possibility of more than one mated *Melittobia* female colonizing a single host is probably not uncommon in nature.

Due to its many bizarre behavioral traits, summarized in Matthews (1997b), and its recent development as a model organism for life science classroom studies (Matthews *et al*. 1996), the genus *Melittobia* has become the subject of relatively large-scale rearing efforts in recent years. However, natural hosts are a relatively difficult food source to obtain commercially for such rearing efforts. A common substitute host for *Melittobia* is the blow fly, *Neobellieria* (= *Sarcophaga*) *bullata* (Parker), but no studies have investigated the effects of using this host on *Melittobia's* biology. This study attempts to address this concern, and examines the development of two species, *Melittobia australica* Girault and *Melittobia digitata* Dahms, when varying numbers of foundress females were provided blow fly puparia as hosts.

Material and Methods

The parasitoids *M. digitata* and *M. australica* reared on *Trypoxylon politum* Say were obtained from cultures maintained in the Laboratory of Insect Behavior of the University of Georgia Entomology Department

Different foundress numbers of mated *M. australica* and *M. digitata* females (< 10 days old) taken from the same source culture were confined in cotton-stoppered two dram glass vials containing one blow fly puparium obtained from Carolina Biological Supply Company, Burlington, NC. The puparia were previously selected to weigh 0.11 g to avoid variation in amount of available host biomass. The treatments consisted of one, two, three, four and five parasitoid females per host, respectively, with 16 replications for each foundress number and species. All cultures were housed in continuous darkness in an incubator maintained at a constant temperature of 25°C. At day 13 after the parasites were placed with the blow fly puparium, the foundress wasps were removed. The puparia continued to be held as described above, and were checked each day for the emergence of flies or wasps.

Records were kept of the number of offspring per treatment, number of descendents per parasitized puparium, developmental duration from puparium exposure to wasp emergence, progeny longevity (deprived of food and host), offspring size, (based on measures of forewing and hind tibia lengths), and offspring morphological form, as determined by the ratio between wing and tibia lengths. One sample of 20 female offspring per each foundress density was taken at random for the measures of the forewing and hind tibia length, which were made using a micrometer scale (0.01 mm) attached to the ocular of a light microscope (10-50x).

Males of *Melittobia* usually do not leave the host cell (Dahms 1984). Thus, two or three days after the last female emergence, the puparia were opened and examined for male presence and the sex ratio (number of females/number of females + males) was calculated.

Analyses of variance and mean comparisons by Tukey HSD tests (P = 0.05) were used to analyze data on developmental time, total number of parasitoids emerged per foundress number, parasitoids emerged per host parasitized, number of parasitoids produced per female within varying foundress number classes, longevity of adults emerged, descendent sex ratios, forewing and hind leg tibia lengths, and the ratio of wing/tibia lengths. A linear regression model was used to compare progeny production, with number of foundresses as the independent variable. All analyses were performed using the Proc GLM of the statistical package SigmaStat 2.0 (1997).

Results and Discussion

A recurring problem with the use of commercially obtained blow fly puparia in our laboratory has been the variable age and condition of these hosts when received. Some blow fly batches exhibit high mortality regardless of whether they are parasitized (Fig. 1), and because the pupae are enclosed within the puparium, their condition cannot be easily preascertained without changing the experimental conditions. For this reason, rather than examining progeny numbers for all the cultures that were set, we report data only when a puparium was successfully parasitized, although this had the unfortunate effect of seriously reducing sample sizes.

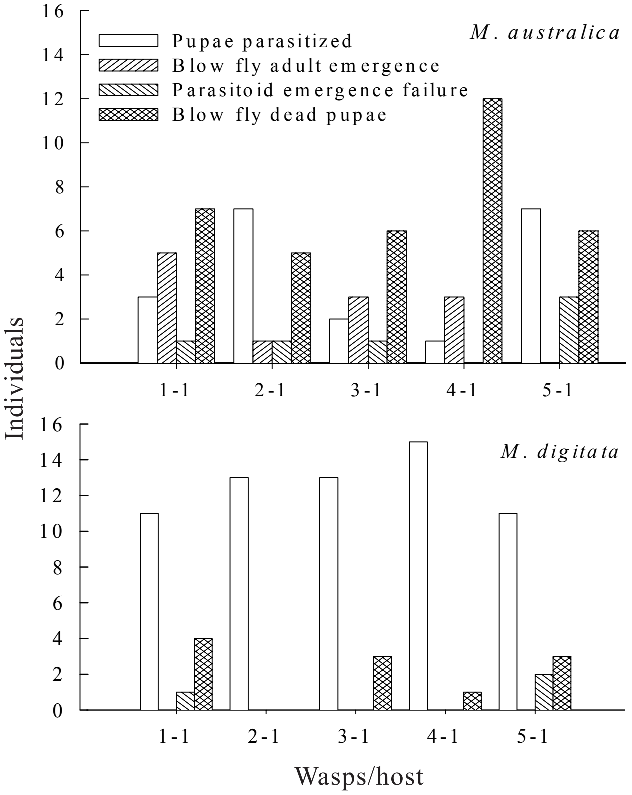

Figure 1. Overall outcome when different foundress numbers of *M. australica* and *M. digitata* were placed with one blow fly puparium of uniform weight.

Host Parasitism. The percentage of puparia parasitized was higher overall for *M. digitata* than for *M. australica* (Fig. 1). In addition, the number of parasitoids that successfully emerged was higher in *M. digitata,* while the number of flies emerging to adults and the number of dead blow fly puparia were higher in *M. australica*.

These data suggest that the blow fly is a relatively better host for laboratory rearing of *M. digitata* than for rearing *M. australica*. The poor performance of *M. australica* may have been exacerbated by poor host quality, as indicated by the high rate of dead puparia. However, if this were true, *M. digitata* should have been similarly affected because hosts were randomly assigned from a single batch of puparia. Further studies are needed to clarify a number of questions about the behavior and development of *M. australica* on blow fly puparia. For example, does this species actually deposit fewer eggs on this host? Or is the host less suitable for larval development? Or do chemicals injected during initial feeding by the foundress change the host's quality or suitability for larval development?

Number of Descendents Produced. Regardless of wasp foundress numbers on one blow fly puparium, the total number of descendents produced by the two species were significantly different (df = 1, 150, F = 75.11, P < 0.001; Fig. 2A). Total progeny ranged from 10.9 to 55.5 for *M. australica*, and from 66.5 to 158 for *M. digitata*. By this measure the latter species is better adapted to use the blow fly as an alternative host. Since adult *M. australica* are measurably smaller than *M. digitata* adults, a blow fly host would be predicted to support the growth of larger numbers of the former, and so this disparity was not expected.

For *M. digitata,* when a puparium was successfully parasitized, increased production of total progeny was observed as function of number of wasps confined per puparium (df = 1, 64, F = 8.21, P = 0.006). However, three foundresses seemed sufficient to fully utilize the host, for at

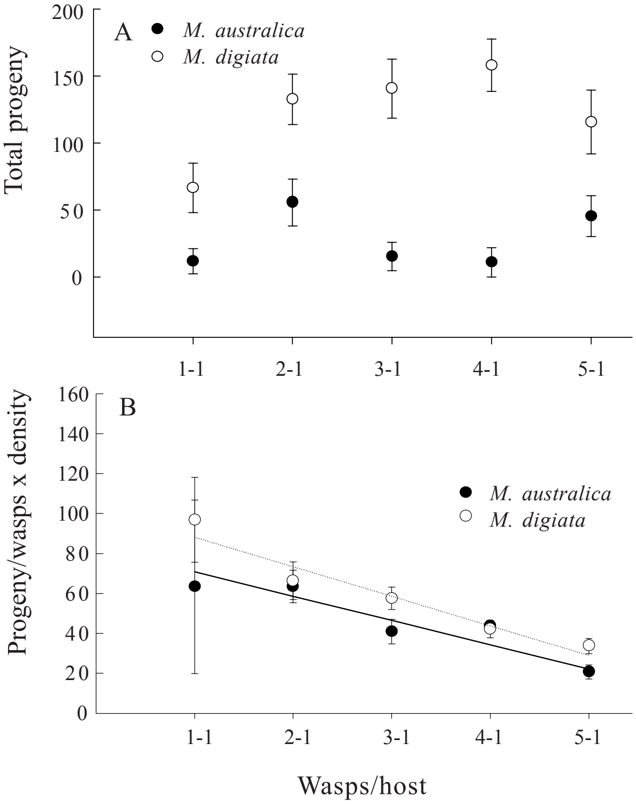

Figure 2. Number of descendents total produced by different numbers of foundresses of *M. australica* and *M. digitata* reared on one parasitized blow fly puparium (A), number of descendents per female within each foundress number class (B).

that point offspring production leveled off and larger foundress numbers did not significantly change total progeny numbers with increasing foundress numbers (Fig. 2A).

For *M. australica,* successful offspring production was more variable, and because of small sample sizes, no significant effect of foundress numbers was observed (df = 1, 18, F = 0.14, P = 0.707). The trend and logic both suggest that a similar flattening off of progeny numbers with increasing foundress numbers may occur. Further studies are warranted to determine the nature and location of this break point.

The number of descendents produced per female was inversely proportional to the number of foundresses on a host, both for *M. digitata* (df = 1, 64, F = 20.04, P < 0.001) and for *M. australica* (df = 1, 18, F = 8.38, P = 0.010; Fig. 2B). Experimental studies of the effect of crowding in *M. australica* (Freeman & Ittyeipe 1976) showed that production of individual offspring is reduced by the crowding of several foundresses on a single host prepuparium. Freeman & Ittyeipe (1993) found that, for *M. australica*, fecundity is probably reduced to about 346 eggs in the field and further to about 298 as a result of superparasitism on *Sceliphron* hosts.

Based on these data, *M. digitata* is the better adapted of the two species when it comes to utilizing blow fly hosts, and that stocking two or three females per host provides maximal production of approximately 170 offspring on a single host. When rearing *M. australica* on this host, theoretically it should be possible to obtain similar numbers, or slightly higher, since it is the smaller of the two species, but more study is warranted.

Developmental Time. Changing the number of foundresses per blow fly puparium significantly affected progeny developmental time for both *M. australica* (df = 3, 16, F = 7.85, P = 0.002) and for *M. digitata* (df = 4, 61, F = 3.22, P = 0.018), as measured from parental host exposure to offspring emergence (Table 1). In general, greater numbers of foundresses per host induced increases in developmental time of *M. australica*, but shortened development times for *M. digitata* (Table 1). This may have been an artifact of the differing offspring numbers produced per parasitized host, since *M. australica* did not show significant increases in progeny at higher foundress numbers, but *M. digitata* did (Fig. 1). The conventional wisdom (reviewed by Cônsoli & Vinson 2002) is that increased competition for nutrients slows development. However, an alternative explanation is that the development of *M. australica* was lengthened by the relative unsuitability of blow fly nutrients for their needs. Comparative studies of *M. australica* development on different hosts would help resolve this question.

Table 1. Developmental time, sex ratio and forewing/hind tibia length ratio of *M. australica* and *M. digitata*, bred from blow fly puparium in different foundress numbers of wasps per puparium

Wasp/host	Developmental time	Sex ratio (female/female+male)	Ratio length W/L (mm)
M. australica			
1:1	26.3 ± 0.37 ab (3)[1]	0.98 ± 0.020 a (3)	3.15 ± 0.05 b (20)
2:1	25.5 ± 0.50 b (8)	0.97 ± 0.010 a (8)	3.26 ± 0.03 a (20)
3:1	25.2 ± 0.11 b (2)	0.97 ± 0.000 a (2)	3.20 ± 0.05 ab (13)
4:1	-[2]	-[2]	3.27 ± 0.13 a (4)
5:1	28.8 ± 0.53 a (8)	0.95 ± 0.030 a (8)	3.17 ± 0.03 b (20)
M. digitata			
1:1	33.6 ± 0.64 a (11)	0.968 ± 0.008 a (11)	3.19 ± 0.02 b (20)
2:1	32.2 ± 0.43 ab (16)	0.968 ± 0.005 a (16)	3.28 ± 0.03 ab (20)
3:1	31.5 ± 0.72 ab (13)	0.971 ± 0.003 a (13)	3.35 ± 0.02 a (20)
4:1	31.3 ± 0.54 ab (15)	0.969 ± 0.002 a (15)	3.34 ± 0.04 a (20)
5:1	30.7 ± 0.25 b (11)	0.956 ± 0.008 a (11)	3.30 ± 0.03 ab (20)

Mean ± SEM followed by the same letter within column do not differ by Tukey HSD test (P = 0.05).

[1]Sample size between parentheses

[2]Number of samples insufficient for analysis

Longevity of Descendents, Size and Morphology. For both *Melittobia* species, increases in foundress numbers on a single host resulted in significantly shorter-lived offspring (df = 4, 198, F = 6.53, P < 0.001; Fig 3). Offspring adult life spans ranged from 6.0 to 9.4 days for *M. australica* and from 2.0 to 8.2 days for *M. digitata*.

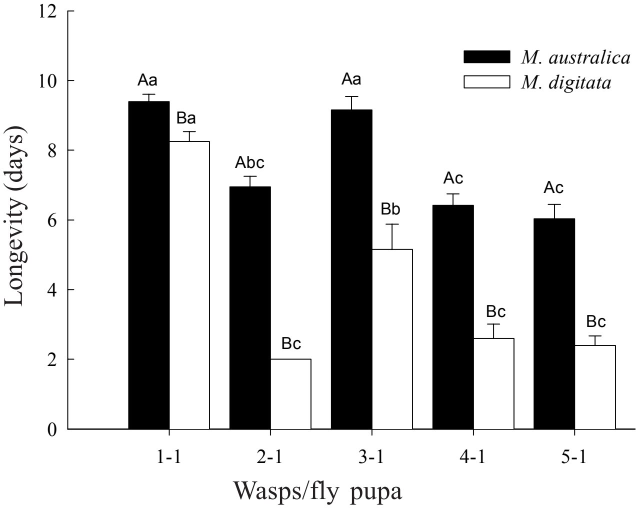

Figure 3. Longevity of *M. australica* and *M. digitata* progeny deprived of food and host when different foundress numbers competed for laying eggs per one host. Bars with the same capital letters do not differ statistically (Tukey HSD test, P = 0.05) between species and by the same small letters between foundress numbers for the same species.

In general, the longevity of *M. australica* descendents was longer than that of *M. digitata* descendents (df = 1, 198, F = 205.57, P < 0.001; Fig. 3). Although longevity is an intrinsic characteristic of a species, the longer life of *M. australica* descendents compared to *M. digitata* might also be a delayed effect of larval development. Adult lives of *M. digitata* may have been shorter because of food competition endured when they were immatures, since *M. digitata* produced more descendents per parasitized puparium (Fig. 1B).

Two different measures (forewing length and hind tibia length) indicated that body size of progeny was significantly reduced by increasing wasp foundress numbers for *M. australica* (forewing, df = 1, 75, F = 136.18, P < 0.001; hind tibia, df = 1, 75, F = 92.33, P < 0.001). The forewing length of *M. australica* varied from 0.81 to 1.03 mm and the hind tibia length from 0.25 to 0.32 mm for individuals emerged from highest to lowest foundress numbers (Fig. 4).

On the other hand, parental foundress numbers did not significantly affect *M. digitata* forewing lengths (df = 1, 98, F = 0.15, P = 0.694); however it affected hind tibia length (df = 1, 98, F = 5.62, P = 0.020). The *M. digitata* forewing and hind tibia lengths ranged from 0.99 to 1.037 mm and 0.29 to 0.32 mm, respectively (Fig. 4).

In general, larger female parasitoids live longer than small ones (Assem *et al.* 1989). In addition, by living longer they can encounter and oviposit in more hosts and their lifetime fecundity will be greater, suggesting that larger females may enjoy higher fitness (Ueno 1999). At present, the place of gregarious idiobiont parasitoids such as *Melittobia* in this picture is unclear. The conventional view has been that their host represents a limited source of nutrients, making clutch size the most important factor in determining the fitness of the next generation (Godfray 1994). The extent to which females choose to leave a fully utilized host in order to search for new hosts to realize their full reproductive potential remains to be investigated.

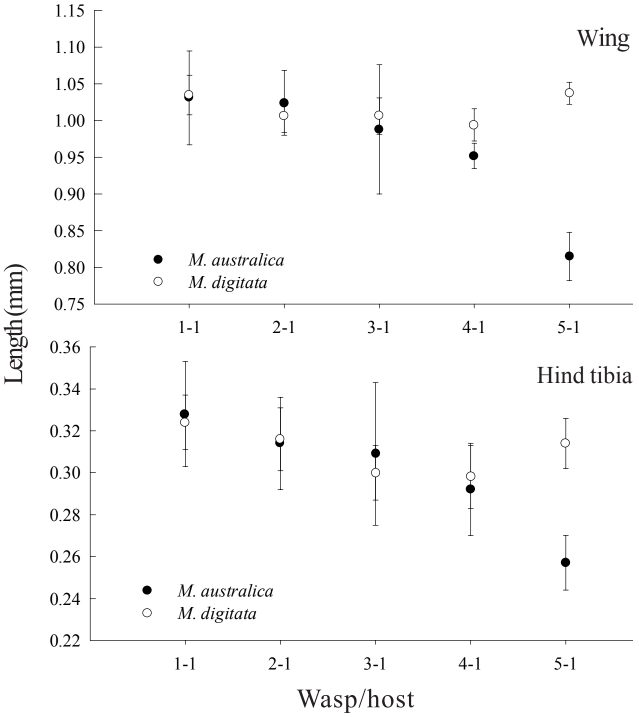

Figure 4. Mean (± SDM) wing and hind tibia lengths for *M. australica* and *M. digitata* offspring parasitizing a blow fly puparium under different foundress numbers.

An interesting twist in the life cycle of some *Melittobia* species is the regular occurrence of two different adult female forms, an early-appearing brachypterous form and a later-appearing macropterous form. Wing polymorphism has been reported in insects in various orders, and in some species has been shown to be density dependent (Zera & Denno 1997). Recent studies by Cônsoli & Vinson (2002) indicate that the change is density-dependent and nutrition-based for *M. digitata* on honey bee hosts. Low larval densities of the parasitoid on honey bee yield short-winged female offspring, whereas high larval densities on the same quality of hosts yield long-winged females. This strategy allows lone colonizing females to utilize a host more fully, via the "multiplier effect" that comes from depositing a stationary generation that immediately begins oviposition on the host, and whose offspring then develop into fully winged dispersive forms.

Cônsoli & Vinson (2002) have used the ratio of forewing to hind tibia length as a standard measure of wing polymorphism and found that this ratio is bimodally distributed, reflecting the brachypterous and macropterous morphs. In the present study, the ratio (forewing/hind tibia) length varied from 3.15 to 3.27 mm for *M. australica,* and from 3.19 to 3.35 mm for *M. digitata*, depending on the number of foundresses per host (Table 1), but there was no consistent trend. It should be noted that blow fly hosts used in this study never yielded any of the brachypterous morph, further evidence in support of the idea that food quality (nutrition) determines developmental pathways in *Melittobia*.

Sex Ratio. Like nearly all Hymenoptera, *Melittobia* practice haplodiploid sex determination; female offspring are the result of fertilized eggs, whereas male offspring arise from unfertilized eggs. The potential for controlling offspring sex ratio in response to environment variables is widespread in the parasitic Hymenoptera (Charnov 1982, Godfray 1994). Host quality factors such as size and age can influence offspring sex ratio (Charnov 1982). West *et al.* (2001) have found that a combination of host size and age influenced the sex ratio strategy of the parasitic wasp *Achrysocharoides zwoelferi* Delucchi (Hymenoptera: Eulophidae). Ueno (1999) has reported that female wasps of *Pimpla nipponica* Uchida (Hymenoptera: Ichneumonidae) adjust offspring sex ratio in response to host size and lay more female eggs in larger and fresher hosts.

Competition from other females for the resources of a constant-weight (0.11g) host presumably would be another relevant environmental variable. However, in our study the number of foundresses per host did not affect the progeny sex ratio for either species to a statistically significant degree (Table 1). Sex ratios ranged from 0.95 to 0.98 for *M. australica* (df = 3, 16, F = 2.12, P = 0.137), and from 0.95 to 0.97 for *M. digitata* (df = 4, 61, F = 0.992, P = 0.419). *Melittobia australica* sex ratio is essentially the same as the one reported by Dahms (1984) on *Sceliphron* spp., other *Melittobia* species have been reported to have similar sex ratios (Dahms 1984), and Buckell (1928) mentions a similar ratio for *M. digitata* (then called *M. chalybii*) using natural hosts.

These results suggest that *M. digitata* has a better development on blow fly puparia than *M. australica* and that three foundresses seemed sufficient to fully utilize the host; however further studies are needed to improve the production of these parasitoid wasps in laboratory on an alternative host.

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