Review of the Biology of *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae) and Additions on Development and Sex Ratio of the Species

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**ABSTRACT.**—A list of known hosts of *Melittobia acasta* and different biological aspects presented in previous literature are summarized and clarified. Development, sex ratio, and offspring production, on wild, facultative, and factitious hosts, and size of stages at different temperatures are shown. In general, development time is equivalent and similar to that of other *Melittobia* species; however, as temperature rises development time decreases. Sex ratio oscillates between 96 to 98% female depending on the host, falling into the expected percentage for most species in the genus. Total offspring numbers were similar to those produced by other *Melittobia* species using the same hosts.

**KEYWORDS.**—development, sex ratio, offspring production

**INTRODUCTION**

*Melittobia* wasps are gregarious ectoparasitoids of wasps and bees especially of those that build mud nests. Before Dahms’ (1984a) revision, the genus consisted of one species native to Europe (*M. acasta*), two native to North America (*M. chalybii* and *M. megachilis*), and a few others from Australia and eastern Asia. After this revision the number of species increased to 14 worldwide. Although *M. acasta* remained the only European species, Dahms also recorded it from Canada, Japan, New Zealand, and South America. For North America, species increased to eight, including *M. acasta*.

Prior to Dahms’ work, for U.S. species the name mostly used in the literature was *M. chalybii*, but these identifications were often erroneous, and as many as 4 species were confused as one (González and Matthews 2002). Likewise, some confusion exists for records of *M. acasta*.

*Melittobia acasta* is reported as a parasite or hyperparasite of members of various orders, including Hymenoptera, Diptera, Lepidoptera and Coleoptera (Table 1). Because it sometimes also attacks bees used for crop pollination such as *Megachile*, *Bombus*, and honeybees (*Apis mellifera*), some research has targeted control aspects (Alford 1975; Dahms 1984b; Doroshina 1990; Erickson & Medenwald 1979; Farkas & Szalay 1985; Fye 1965; Herting 1977; Holm 1960; Holm & Skou 1972; Husband & Brown 1976; Jelinski & Wojtowski 1984; Kalinin & Molchanov 1987; MacFarlane & Donovan 1989; MacFarlane & Griffin 1994; MacFarlane & Palma 1987; MacFarlane et al. 1994; Maeta 1978, 1985, 1999; Packard 1864; Pourreau 1973; Santis 1981; Schmid-Hempel 1998, 2001; Smith 1853; Stolvov & Palevich 1988; Thompson 1946; Torchio 1963; Valkeila 1959; Wael et al. 1993, 1995; Zerova et al. 1986).

Other studies emphasized, evolutionary, morphological, biological and behavioral aspects, especially those related to courtship, with *M. acasta* serving as a model or compared with other species (Alston 1920; Assem 1975, 1976a, 1976b, 1985; Assem & Maeta 1978; Assem et al. 1982; Balfour-Browne 1922; Borgia 1980; Dahms 1984b; Doroshina 1989; González 1994a, 1994b; González & Matthews 2002; González & Terán 2001; González et al. 1996, 1999, 2004; Klunker & Fabritius 1992; Lapp 1994; Lith 1955; Malyshev 1968; Nong & Sailer 1986; Parker & Thompson 1928; Picard 1922,
Through careful reading of the older primary literature coupled with study of museum voucher materials and controlled laboratory studies, we are attempting to untangle some of the confusion surrounding species identity in *Melittobia*. Results will help to promote nomenclatural stability and thereby facilitate future work on this interesting genus. Here we focus on the widespread *M. acasta*.

**MATERIALS AND METHODS**

In order to compare the status, distribution, and other aspects related to the biology of *M. acasta*, a thorough literature review was done. Laboratory studies were

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**TABLE 1. Reported hosts of *Melittobia acasta* (Walker)**

<table>
<thead>
<tr>
<th>Host group</th>
<th>Countries</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Social Bees (<em>Bombus</em> spp.; <em>Apis</em> spp.)</td>
<td>Great Britain; New Zealand</td>
<td>Alford 1975; Balfour-Browne 1922; Erickson &amp; Medenwald 1979; Hobbs &amp; Krum (1971); MacFarlane &amp; Donovan 1989; MacFarlane et al. 1994; Valkeila 1959; Wael et al. 1993, 1995</td>
</tr>
<tr>
<td>Parastatic Bees (<em>Psyttirus</em> spp., <em>Stelis</em> spp.)</td>
<td>Great Britain; Germany</td>
<td>Alford 1975; Wolff &amp; Krausse 1922</td>
</tr>
<tr>
<td>Solitary Bees (<em>Anthophora</em> spp., <em>Chalicodona</em> sp., <em>Herales</em> spp.; <em>Anthidium</em> sp.; <em>Megachile</em> spp.; <em>Osmia</em> spp.)</td>
<td>Great Britain; Russia; USA; New Zealand; Japan; Finland</td>
<td>Balfour-Browne 1922; Doroshina 1989, 1990; Farkas &amp; Szalay 1985; Herting 1977; Holm &amp; Skou 1972; MacFarlane &amp; Donovan 1989; Maeta 1985; Smith 1853; Thompson 1950a; Valkeila 1959</td>
</tr>
<tr>
<td>Mud dauber wasps (<em>Trypoxylon</em> spp., <em>Sceliphron</em> spp.)</td>
<td>Great Britain; Cuba; Venezuela; Japan</td>
<td>Balfour-Browne 1922; Dahms 1984b; González 1994a, 1994b; González &amp; Terán 1996; González et al 2004; Maeta 1985</td>
</tr>
<tr>
<td>Parasitic wasps (<em>Alysia</em> mandiculator; <em>Monodontomerus</em> spp.; <em>Sinothorax turionus</em>; <em>Sphecoptera vesparium</em>; <em>Chrysis</em> spp.)</td>
<td>Great Britain; Japan; New Zealand; Germany</td>
<td>Alson 1920; Balfour-Browne 1922; Dahms 1984b; Donovan 1989; Maeta &amp; Yamane 1974; Wolff &amp; Krausse 1921, 1922; Husain &amp; Khan 1986; Thompson 1950a</td>
</tr>
<tr>
<td>Other solitary wasps (<em>Ancistrocerus</em> spp., <em>Odynerus</em> spp.)</td>
<td>Germany; Finland</td>
<td>Herting 1977; Lith 1955; Wolff &amp; Krausse 1922; Malyshov 1911, 1968</td>
</tr>
<tr>
<td>Social wasps</td>
<td>Great Britain; Japan</td>
<td>Bouček 1959; Maeta 1985; Maeta &amp; Yamane 1974</td>
</tr>
<tr>
<td>Flies and parasitic flies (<em>Musca</em> spp.; <em>Neobellieria</em> spp.; <em>Sarcophaga</em> spp.; <em>Calliphora</em> spp.; Anthrax spp.; <em>Metagonistylum minense</em>; <em>Paratheresia claripalpis</em>)</td>
<td>Great Britain; Japan</td>
<td>Dahms 1984b; Graham-Smith 1916, 1919; Herting 1978; Maeta &amp; Yamane 1974; Waterston 1917</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>Great Britain</td>
<td>Herting 1975; Morley &amp; Rai; Thompson 1950b</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Czechoslovakia</td>
<td>Bouček 1959</td>
</tr>
</tbody>
</table>
initiated using *M. acasta* originally collected in Venezuela (Assays 1-4) or California, U.S.A. (Assay 4). Unless otherwise noted, cultures were established in 2-dram vials and maintained at 25°C and 70% RH.

Assay 1: In order to see if hosts [*Sceliphron fistularium* (Hymenoptera: Sphecidae)] could survive and develop if parasitoids were removed, individual mated females of *M. acasta* were allowed to lay about 100 eggs/host (n=100). Females were then removed and a few days later developing third instar *M. acasta* larvae were removed from every host.

Assay 2: To assess whether temperature had any influence on size, regular cultures were established on *S. fistularium* at different temperatures (15°C, 20°C, 25°C, 30°C, and 35°C) and 70% RH. Length and width of eggs, all larval instars, and pupae were measured of a sample from the whole offspring produced (Brood size approximately 400-500 individuals per host; Sample size: n=39 for each stage and temperature). Egg widths were measured at two places (small and large width) because of their "pear-like" shape. Larval width was measured at the mid part of the body, and pupae were measured at the junction of the thorax and abdomen. Measurements were taken using a stereoscope adapted with an ocular micrometer.

Assay 3: To study duration of each life stage and instar of *M. acasta*, parasitized *S. fistularium* hosts were maintained at various temperatures (15°C, 20°C, 25°C, 30°C, and 35°C) and 70% RH (n=20/each temperature). Observations were made every 12 hours and the developmental stage was recorded. Sample individuals were removed (see assay 2) for measurements and to determine if they had passed to the next instar.

Assay 4: In order to compare development time and sex ratio of *M. acasta* on different hosts, cultures of the parasitoid were made using as hosts: *S. fistularium* (n=90), *Trypoxylon politum* (n=40), *Megachile rotundata* (n=40), *Neobellieria bullata* (n=40). One female of *M. acasta* was placed per host. Life history was followed to determine duration of each developmental stage. Offspring were counted to determine sex ratio.

All experiments using *S. fistularium* as hosts were conducted in climatically controlled chambers at Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela. Experiments with other hosts (assay 4) were done in incubators at University of Georgia, Athens, Georgia, U.S.A.

RESULTS

Although some authors (Eickwort 1971, 1973; Hobbs & Krunic 1971; Holm 1960; Husband & Brown 1976; MacFarlane & Pengelly 1977; Maeta & Yamane 1974; Newport 1849a, 1849b, 1852a, 1852b, 1853; Packard 1864; Spradbery 1973; Thomson 1878; Wolff & Krausse 1921) mentioned *Melittobia* or related species in their work, after careful analysis of those works and available voucher specimens we conclude that they were often working on (or found) *M. acasta* (Dahms 1984a; González & Matthews 2002).

When females of *M. acasta* are presented with a suitable host (i.e., *Sceliphron* spp., *Trypoxylon* spp.), they wander around it, and after some time spent (1-48 h) "assessing" the host, they puncture the host’s exocuticle with their ovipositor. After a few seconds, hemolymph starts to ooze from the wound, upon which the female then feeds.

Females become distinctly physogastric 12-48 hours after first feeding. Beginning 12 to 24 hours after feeding, most females start laying eggs (Table 2). Eggs are coated with a sticky substance that allows them to adhere to the host and to other eggs. Eggs are normally laid in batches of 4 to 12, however lower egg numbers or individually deposited.

<table>
<thead>
<tr>
<th>Host</th>
<th>Eggs (days)</th>
<th>Larvae (days)</th>
<th>Pupae (days)</th>
<th>Total (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sceliphron fistularium</em></td>
<td>1-3</td>
<td>14-16</td>
<td>3-5</td>
<td>18-24</td>
</tr>
<tr>
<td><em>Trypoxylon politum</em></td>
<td>2-4</td>
<td>9-15</td>
<td>6-8</td>
<td>17-27</td>
</tr>
<tr>
<td><em>Megachile rotundata</em></td>
<td>2-5</td>
<td>8-14</td>
<td>5-8</td>
<td>15-27</td>
</tr>
<tr>
<td><em>Neobellieria bullata</em></td>
<td>2-7</td>
<td>8-12</td>
<td>5-9</td>
<td>15-28</td>
</tr>
</tbody>
</table>

TABLE 2. Life history development of *Melittobia acasta* on different hosts at 25°C. (S.f. n = 90, 50% RH; other hosts n = 40, 50% RH)
ited eggs are not rare. The female initially lays eggs on the ventral region of the host, but eventually covers other areas of the host body.

Two female morphs (brachypterous and macropterous) exist (González & Terán 1996; González et al. 1996), and although they differ in some particular behaviors (courtship, migration tendencies), their egg laying behavior was basically identical. The main difference is that brachypterous females deposit eggs immediately upon emergence and mating.

After removing all the *M. acasta* larvae from 100 parasitized *S. fistularium* prepupae (Assay 1), 14 hosts were found to have black spots or darkened wound marks, presumably caused by the female’s ovipositor. None of these hosts developed, while the others died. Out of the 100 hosts, 73 became apparently normal adult *S. fistularium*, with the other 13 succumbing to fungi.

Eggs hatched between 1-3, 2-4, and 2-7 days in *S. fistularium*, *T. politum*, and *N. bullata* respectively (Table 2). Larval and pupal development also varied with host type (Table 2). Offspring numbers and sex ratio varied among the hosts (Table 3).

Eggs hatch between 12 to 48 hours, depending on the temperature (Table 4), and have an average length of 0.21 mm (Table 5). The large egg width averages 0.06 mm and the smaller width averages 0.04 mm regardless of temperature (Table 5). First instar larvae are easily recognized by the apparent body segmentation and they are similar in length to the eggs (Table 5). The second and third instars are recognized not only by the difference in size, but because just after molting the last larval "skin" is attached to the distal end of the body. They also molt at different times depending on the temperature (Table 4). Fourth instar larvae have a slower development, and they take on the color of the host they are feeding on. All larvae are vermiform and the main difference between instars is their size (Table 5). At 15°C, second instar larvae entered diapause; after 10 months, these diapausing larvae were placed at 25°C, and most resumed normal development and became adults.

Pupae appear 10 to 15 days after the eggs are laid (Tables 2). They are exaerete and measure about 1.5 mm long and 0.5 mm wide, regardless of temperature (Table 5). Pupae are creamy-white and darken as they mature. Males are brownish, and have red “dots” where the eyes should be. Female eyes become pink and later red, while the body gets dark brown-black. Males become shiny dark brown, females shiny black when close to emerging as adults.

Males are the first adults to emerge, a group of brachypterous females emerges after that, and macropterous females emerge last. Some males were observed fighting, and in most cases the first to emerge killed some male pupae that were almost ready to become adults.

**DISCUSSION**

*Melittobia acasta* appears to be the only *Melittobia* species present in Europe (including Russia) but it is also found in Argentina, Canada, Costa Rica, Cuba, India, Japan, New Zealand, Australia, U.S.A., and Venezuela (Table 1). Torchio (1963); Hobbs & Krunic (1971); and Husband & Brown (1976) mention that they found *M. chalybii* attacking *Megachile rotundata* in some areas of USA and Canada. However, according to descriptions and places mentioned it is likely that they were actually dealing with *M. acasta*. Moreover, MacFarlane & Griffin (1994) mention that “according to Matthews’ Husband & Brown (1976) mention that they found *M. chalybii* attacking *Megachile rotundata* in some areas of USA and Canada. However, according to descriptions and places mentioned it is likely that they were actually dealing with *M. acasta*. Holm (1960) mentions *M. chalybii* attacking *Bombus* colonies in Denmark. Because of this location, we suspect that they actually found *M. acasta*, which the same author and a collaborator found later attacking *Megachile* species (Holm & Skou 1972).
Melittobia acasta is clearly capable of parasitising a wide variety of insects belonging to different orders (Table 1), although it seems unlikely that this broad range of hosts attacked would be noticed under field conditions. The fact that several species of pollinators are apparently regularly attacked by *M. acasta* should be of concern, especially where populations of these pollinators are artificially manipulated. The importance of *M. acasta* in these situations merits further study, because populations can build to high levels in a relatively short time due to the rapid development time of this gregarious parasitoid.

Parker & Thompson (1928) could not stimulate females of *M. acasta* to feed on honey or sugar water at different concentrations; however, this was done in our laboratory with *M. digitata* and *M. australica* (L.Deyrup pers. comm.). Host feeding by female *Melittobia acasta* is very similar to that observed in other *Melittobia* species as reported by different authors (Balfour-Browne 1922; Coënsoli and Vinson 2001; Dahms 1984b; Malyshev 1968; Maeta & Yamane 1974; Schmieder 1933). After puncturing the host cuticle with her sting, females of *M. acasta* feed on the oozing hemolymph, as do most idiobionts. According to Doutt (1959) host fluids provide the proteins necessary to stimulate egg development. However, while host feeding is common among macropterous females, it is not for the brachypterous females. The latter emerge with a large load of eggs and

### Table 4. Time ranges (hours) for each developmental stage in *Melittobia acasta* (Walker) developing on *S. fistularium* at different temperatures (n = 20 hosts/temperature).

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Egg</th>
<th>1st instar (larvae)</th>
<th>2nd instar (larvae)</th>
<th>3rd instar (larvae)</th>
<th>4th instar (larvae)</th>
<th>Pupae</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>36-60</td>
<td>36-60 **</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>12-36</td>
<td>36-60</td>
<td>60-84</td>
<td>60-84</td>
<td>216-264</td>
<td>96-144</td>
<td>480-672</td>
</tr>
<tr>
<td>25</td>
<td>12-36</td>
<td>12-36</td>
<td>36-60</td>
<td>36-60</td>
<td>216-264</td>
<td>72-120</td>
<td>384-576</td>
</tr>
<tr>
<td>30</td>
<td>8-20</td>
<td>6-20</td>
<td>6-18</td>
<td>36-60</td>
<td>192-240</td>
<td>72-120</td>
<td>320-478</td>
</tr>
<tr>
<td>35</td>
<td>8-20</td>
<td>6-20</td>
<td>6-18</td>
<td>12-36</td>
<td>12-36</td>
<td>72-120</td>
<td>116-250</td>
</tr>
</tbody>
</table>

### Table 5. Size of different stages of *Melittobia acasta* (Walker) on *Sceliphron fistularium* (Dahlbom) at different temperatures. (X ± SD; n = 39 larvae measured/temperature). Relative Humidity: 70%)

<table>
<thead>
<tr>
<th>Temp. °C</th>
<th>Eggs</th>
<th>Development Stages</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Larvae 1st instar</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td>.21 ± .004</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Length</td>
</tr>
<tr>
<td>20</td>
<td></td>
<td>.21 ± .003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Length</td>
</tr>
<tr>
<td>25</td>
<td></td>
<td>.21 ± .003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Length</td>
</tr>
<tr>
<td>30</td>
<td></td>
<td>.21 ± .003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Length</td>
</tr>
<tr>
<td>35</td>
<td></td>
<td>.21 ± .002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Length</td>
</tr>
</tbody>
</table>

*: Two widths were measured in eggs. The first refers to the larger one; In larvae and pupa it refers to the only one measured.

**: 2nd instar larvae remained in diapause at 15°C.
start laying them immediately after mating, similar to M. digitata (Cónsoli and Vinson
2001).

Maeta and Yamane (1974) reported darkening of hosts wounds made while feeding
by the ovipositor of M. japonica (=M. acasta). In our experiments only 14, out of 100
hosts, S. fistularium prepupae’s sting marks were darkened, and none of these were
able to pupate and develop into normal adults. This sting mark also was found in
Tenebrio molitor pupae attacked by M. digitata, and such hosts seldom developed into
adults (Deyrup et al. 2003). Trypoxylon politum prepupae did not show evidence of
melanization at sting sites. Since the last larval skin surrounds Neobellieria bullata pu-
pae, we do not know whether this occurs in this host. The striking thing is that, except
for mortality due to fungi, all 75 out of 100 parasitized prepupae of S. fistularium that
did not show sting mark evidence were subsequently able to pupate and develop into
apparently normal adults.

When stinging their host, M. acasta fe-
male could also inject fluids whose effect
is to diminish body movements, stop host
development, or both, as Malyshev (1968)
suggested. Buckell (1928) observed a simi-
lar situation working with M. chalybii (=M.
digitata), a species that is closely related to
M. acasta (Assem et al. 1982; Dahms 1984b).
It appears that substances injected during
host stinging by M. acasta vary in their ef-
fects on host physiology and development
and that further study of the venom and
accessory gland materials would be re-
warding.

When temperature is controlled, hatch-
ing time and total development time can be
artificially modified. At 15°C (70% RH),
eggs hatch about 48 hours after being laid,
but as temperature increases, hatching time
diminishes to about 12 hours (Table 4). The
same trend is found for every developmen-
tal stage of M. acasta, resulting in a faster
total development time with higher tem-
perature (Table 4). However, at 15°C (70%
RH), after entering the second instar, larvae
of M. acasta remained in diapause, and ter-
minated only when the temperature was
increased. Diapause regulation in M. acasta
is wholly unstudied, but since this species
occurs widely under a broad range of en-
vironmental conditions from tropical to tem-
perate regions, the cues involved in dia-
pause merit further study. Even though the
total development increases when tempera-
ture increases (Table 4) the size of the dif-
ferent stages of M. acasta remain the same
(Table 5).

Two female morphs are commonly
found in all Melittobia species (Cónsoli &
Vinson 2002a, 2002b; González & Terán
1996; González et al. 1996; Schmieder 1933).
Lith (1955) reported the presence of 1% of
brachypterous females and termed them “a
genetical anomaly.” Morphological and be-
havioral characteristics of males and the
two female morphs of M. acasta and M. aus-
tralica were described by González & Terán
(1996), González et al. (1996) compared
courtship behavior among morphs of M.
acasta and other Melittobia species. Brachy-
pterous females represent about 1-2% of
the total females produced by M. acasta on
S. fistularium, T. politum and M. rotundata
hosts. No brachypterous females were pro-
duced on Neobellieria bullata.

Development time varied slightly de-
pending on the host (Table 2). The same can
be said about the total clutch size and sex
to 0.92, and the size of the total females pro-
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Central de Venezuela (TPG A-03787). Part was also supported by NSF Grant 0088021, R.W. Matthews, principal investigator.

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MELITTIOBIA ACASTA (HYMENOPTERA) 59


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