The Great Lakes Entomologist

Volume 35
Number 1 - Spring/Summer 2002 *Number 1 - Spring/Summer 2002*

Article 15

April 2002

Development and Sex Ratio of *Melittobia Australica* and *M. Digitata* (Hymenoptera: Eulophidae) on *Megachile Rotundata* (Hymenoptera: Megachilidae) and *Trypoxylon Politum* (Hymenoptera: Sphecidae)

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DEVELOPMENT AND SEX RATIO OF MELITTOBIA AUSTRALICA AND M. DIGITATA (HYMENOPTERA: EULOPHIDAE) ON MEGACHILE ROTUNDATA (HYMENOPTERA: MEGACHILIDAE) AND TRYPOXYLON POLITUM (HYMENOPTERA: SPHECIDAE)

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ABSTRACT

Life history, development time, and sex ratio of *Melittobia australica* Girault and *M. digitata* Dahms on *Megachile rotundata* (Fabricius) and *Trypoxylon politum* Say are presented and compared with previous reports. Total development time and sex ratio differs slightly amongst the different hosts but falls within the expected range reported for different hosts and *Melittobia* species. The slightly longer development times and higher proportion of males recorded for both species on *M. rotundata* hosts probably reflects poorer host nutritional quality, relative to *T. politum*. We confirm that the one unusually extended development time reported by Schmieder for *Melittobia chalybii* Ashmead collected in New Jersey, can be accounted for as likely having represented a previously unknown species since described as *M. femorata* Dahms.

Melittobia wasps (Hymenoptera: Eulophidae) are arrhenotokous parasitoid wasps normally associated with mud dauber wasps (Hymenoptera: Sphecidae) of the genera *Trypoxylon* and *Sceliphron*. However, many bees, wasps, and even insects of different orders have been reported to be attacked by these parasitoids (Dahms 1984b, Girault 1912, González and Terán 1996, Howard 1892, Maeta and Yamane 1974, Matthews et al. 1996).

Even though *Melittobia* spp. can be relatively easily cultured in the laboratory on mud dauber wasp prepupae (*Trypoxylon* spp. and *Sceliphron* spp.), it is relatively difficult to obtain numerous hosts. Some researchers have used honeybee prepupae as hosts with complete success (Cônsoli and Vinson 2002a, 2002b, Varanda et al. 1984). Others have used puparia of different flies as hosts (Balfour-Browne 1922, Matthews et al. 1996). Some *Melittobia* spp. can be reared on puparia of flesh flies, *Neobellieria bullata* (Parker), (Diptera, Sarcophagidae), which is how the WOWbug (*Melittobia digitata*) is commercially reared (Matthews et al. 1996, Cônsoli and Vinson 2002a, 2002b).

Even though some *Melittobia* species have been reported as pests of *Megachile* spp. and especially of the leaf–cutter bee, *Megachile rotundata* (Fabricius), by various authors in different regions (Edwards and Pengelly 1966, Farkas and Szalay 1985, Peck 1969, Tasei 1978, Woodward 1994) no information exists concerning development time and sex ratio of *Melittobia* spp. on this host. Furthermore, while the pipe-organ mud dauber wasp, *Trypoxylon politum* Say, and other species in this genus also have been reported as hosts of a few *Melittobia* species (Buckell 1928, González and Terán 1996, González et al. 1985, Lith 1955, Matthews et al. 1985, Schmieder 1933, 1938) there is only one brief mention in the literature for development time and sex ratio of *Melittobia digitata* Dahms on *T. politum* (Matthews et al. 1996), and nothing for *Melittobia australica* Girault. The objective of the present study is to provide information on these aspects of the biology of *M. australica* and *M. digitata* reared on *M. rotundata* and *T. politum* prepupae under uniform conditions.

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MATERIALS AND METHODS

Melittobia australica and *M. digitata* were reared on prepupae of *M. rotundata* and *T. politum*. *Trypoxylon politum* hosts were collected as diapausing prepupae from the vicinity of Athens, GA and kept refrigerated until use. *Megachile rotundata* were obtained as diapausing cocoons from Ron Bitner (Pioneer Hybrid International, Namper, ID) and also kept refrigerated until use. For rearing each species of *Melittobia* a single host (of both host species) was removed from its cocoon and placed in a clear-view polystyrene chamber (15 mm x 20 mm x 45 mm) with 1 , 2 or 3 mated *Melittobia* females per host. Forty replicates on each host were simultaneously started for each *Melittobia* species under study. Hosts of both species were taken from the same batches, kept in a refrigerator, and were presumably the same age. Hosts were weighed and only those weighing 0.30 g (*T. politum*) and 0.03 g (*M. rotundata*) were used for this study. Cultures were reared at 25° C and 50 % RH in an incubator.

Duration, in days, of development from egg to larvae, from larvae to pupae, and from pupae to imago, was determined through daily observations and reported as ranges. Final progeny counts were used to determine sex ratio.

Data are compared with information from other *Melittobia* species and hosts that have been previously published.

RESULTS AND DISCUSSION

As on other prepupae of different wasps and bees, both *M. australica* and *M. digitata* laid clusters of eggs mainly along intersegmental grooves but not restricted to any particular area of the host (Dahms 1984b, González 1994). In both *Melittobia* species, eggs hatched between 2 and 4 days on both hosts, which is typical for most *Melittobia* species reared at temperatures between 20 and 25 ° C (Table 1). The larvae of *M. australica* became pupae after 8 – 14 days on *M. rotundata*, but slightly earlier (7 – 11 days) on *Trypoxylon politum*. The same trend was found in *M. digitata,* which became pupae between 9 –12 days on *M. rotundata* and 7 – 9 days on *T. politum*. *Melittobia australica* eclosed as adults after 5 – 8 days as pupae on *M. rotundata* and 5 – 7 days as pupae on *T. politum*. A similar overall pattern of slightly faster development on *T. politum* hosts was exhibited by *M. digitata* (Table 1).

Most studied *Melittobia* species have larval stages that last 7 – 15 days before transforming into pupae, except for *M. hawaiiensis* whose larval development time varies between 5 – 7 days and *M. acasta* that can require up to 18 days (Table 1). A curious case is *M. chalybii* reported by Schmieder (1933) in which the larval stage lasted up to 71 days; we will address this later. The pupal stage lasts between 4 to 8 days in most studied species. However in *M. acasta* reared at 25 º C some require as few as 3 days and in *M. chalybii* the pupal stage may last up to 15 days (Table 1).

Cônsoli and Vinson (2002a, 2002b) have suggested that nutritional quality of the host can dramatically affect development time in *M. digitata*. Specifically, they show that larvae reared primarily on host hemolymph develop faster than those that feed on the remaining host tissues having correspondingly less hemolymph. This finding suggests a basis for the slightly longer development times we found for both *Melittobia* developing on *M. rotundata* compared to *T. politum*. The prepupae of *M. rotundata* are less than half as large as those of *T. politum*, and are not nearly as flaccid which probably reflects reduced availability of hemolymph, thereby forcing the developing *Melittobia* to cope with a less optimal diet. This ultimately results in a greater proportion of the long-wing morph relative to the short-wing (brachypterous) form on *M. rotundata* and the former require longer to develop (Cônsoli and Vinson 2002).

Table 1: Summary of published life history development time of different *Melittobia* species on various hosts at different places and temperatures. Values are averages or ranges.

***Melittobia* Species**	**Host**	**Temp (°C)**	**Eggs (Days)**	**Larvae (Days)**	**Pupae (Days)**	**Total (Days)**	**Country**	**Reference**
australica	*Megachile rotundata*	25	2 – 4	8 – 14	5 – 8	15 – 26	USA	This study
australica	*Trypoxylon politum*	25	2 – 4	7 – 11	5 – 7	14 – 22	USA	This study
digitata	*Megachile rotundata*	25	2 – 4	9 – 12	5 – 8	16 – 24	USA	This study
digitata	*Trypoxylon politum*	25	2 – 4	7 – 9	5 – 8	14 – 21	USA	This study
acasta	*Sceliphron fistularium*	20	2 – 3	16 – 18	4 – 6	23 – 27	Venezuela	González, 1994
acasta	*Sceliphron fistularium*	25	1 – 3	14 – 16	3 – 5	18 – 24	Venezuela	González, 1994
acasta	*Odynerus* spp., *Trypoxylon* spp.	18 – 19	3 – 4	11 – 15	7 – 8	21 – 27	Finland	Lith, 1955
acasta	Various Hymenoptera	26	1 – 2	6 – 13	3 – 10	10 – 24	Japan	Maeta, 1978
acasta	Various Diptera and Hymenoptera	?	2 – 7	8 – 9	7	17 – 23	England	Balfour-Browne, 1928
australica	*Sceliphron formosum*	25 – 30	3 – 4	8 – 10	3 – 4	14 – 18	Australia	Dahms, 1984b

Table 1: Continued

Melittobia **Species**	**Host**	**Temp (°C)**	**Eggs (Days)**	**Larvae (Days)**	**Pupae (Days)**	**Total (Days)**	**Country**	**Reference**
chalybii (2 - 4 spp.)*	*Trypoxylon politum*	19 – 25	4	7 – 71	3 – 15	14 – 90	USA	Schmieder, 1933
chalybii (=*digitata*)	*Trypoxylon politum*	?	3 – 4	11 – 15	7 – 8	21 – 27	USA	Buckell, 1928
digitata	*Trypoxylon politum*	22 – 30	3 – 4	7 – 10	4 – 7	14 – 21	USA	Matthews *et al.*, 1996
digitata	*Neobellieria bullata*	22 – 30	3 – 4	7 – 10	4 – 7	14 – 21	USA	Matthews *et al.*, 1996
hawaiiensis	*Apis mellifera*	?	1 – 2	5 – 7	5 – 7	11 – 16	Brasil	Varanda *et al.*, 1984

* Schmieder (1933) presents drawings of *M. chalybii*, but mentions different localities including the one from which *M. evansi* was later described. He also notes the occurrence of a "diapausing *Melittobia*" and suggests that it is related to "trophic conditions obtained during the larval growth". Part of Schmieder's material was also used by Whiting (1947), who mentions the use of four *Melittobia* species and shows a photograph of *M. digitata*. See text for further details.

Arrhenotokous insects with extreme inbreeding normally have female-biased ratios (Assem et al. 1982, Dahms 1984b, Hamilton 1967). The sex ratio of different *Melittobia* species has been reported by many authors as highly skewed toward females, with the percentage of males varying from 1 – 5 % (Table 2) regardless of host used. Unlike some other species of parasitoid wasps (reviewed by Godfray 1994) *Melittobia* females do not adjust their sex ratio in response to the number of foundress females. Although more individuals were produced in the larger host, sex ratios were basically the same when 1, 2 or 3 female foundresses were used in each *Melittobia* species on each host. Brachypterous females were also produced on both hosts but their number varied (decreasing as the number of foundresses increased). Data on these aspects will be presented elsewhere.

When sex ratio is compared in the two *Melittobia* species used in this study on the two different hosts the percentage of males was slightly higher when reared on *M. rotundata*(Table 2) . One possible explanation is that on *M. rotundata* "late" developing individuals fail to survive due to active or passive interference by their siblings, including facultative siblicidal behavior as shown by Cônsoli and Vinson (2002a). This would disproportionately affect females, since males develop slightly faster, causing the sex ratio to be slightly more male-biased. Adams (2002) has shown that males are laid at a relatively constant daily rate throughout the foundresses' tenure on the host. It is also possible that the relatively poorer host quality of *M. rotundata* affected the final sex ratio.

Table 2: Sex ratios of different *Melittobia* species compared from this study and the literature.

***Melittobia* species**	**Host**	**Male - Female Ratio and range**	**Reference**
australica	*Megachile rotundata*	5:95 (4 – 8):(96 – 92)	This study
australica	*Trypoxylon politum*	2:98 (1 – 3):(99 – 97)	This study
digitata	*Megachile rotundata*	4:96 (3 – 5):(97 – 95)	This study
digitata	*Trypoxylon politum*	2:98 (1 –3):(99 – 97)	This study
acasta	*Sceliphron fistularium*	(3 – 5):(97 – 95)	González, 1994
australica	Sceliphron *formosum*	(1 – 4):(99 – 96)	Dahms, 1984b
chalybii (= 3 diff. spp.)*	*Sceliphron* sp., *Chalybion* sp., *Trypoxylon* sp	3:97	Schmieder, 1938
digitata	*Trypoxylon politum*	5:95	Matthews *et al.*, 1996
digitata	*Trypoxylon politum*	2.4:97.6	Adams 2002
hawaiiensis	*Apis mellifera*	2:98 (1 – 3):(99 – 97)	Varanda *et al.*, 1984

* In this paper, Schmieder mentions that he was working with probably three species that when intercrossed did not "…produce any female offspring…" but were "cytologically, like *chalybii*". See text for further details.

Schmieder (1933) reared *M. chalybii* between 19 – 25 º C and recorded a life cycle of up to 90 days with a larval stage lasting up to 71 days. Dahms (1984b) mentioned that these times seemed excessive, but did not offer an explanation. Schmieder (1939) suspected that he had been working with either two or three different species, even though he mentioned them only as *M. chalybii*. Whiting (1947) mentions that Schmieder was probably rearing as many as four different species. After carefully reviewing Schmieder's papers (1933, 1938, 1939) and one by Whiting (1947) we suspected that he was working with at least three different species, and possibly as many as four (which we believed were *M. chalybii*, *M. evansi, M. digitata,* and *M. femorata*). According to Dahms (1984a), *M. chalybii* is reportedly common from the New Jersey area where Schmieder worked. *Melittobia evansi* was described by Dahms (1984a) from specimens that came originally from our laboratory in Athens, GA, and also from Goshen, N.J. reared by Schmieder. The third species, *M. digitata*, also described by Dahms (1984a), appears in a photograph in Whiting (1947) credited as from Schmieder's cultures. The male in the photograph clearly exhibits the scape morphology characteristic of *M. digitata*.

The fourth species, *M. femorata,* is a common species in Georgia, Alabama, North and South Carolina, but also occurs in New Jersey, and we have also collected it in West Virginia, Virginia, Kentucky, Ohio and Michigan. As yet it is poorly studied. However, we have maintained it in the laboratory for several years. Even at a constant temperature of 25º C, it has an obligatory prepupal diapause on *T. politum* hosts that lasts for several weeks, and is the only *Melittobia* species we know with this life history variation. Thus, its total life history could easily last 90 days or longer. Recently, we were able to study voucher specimens from Schmieder's and Whiting's research deposited at the Smithsonian Institution (NMNH). These confirmed our suspicions; some specimens labeled as *M. chalybii* actually are *M. evansi, M. digitata* and *M. femorata*.

ACKNOWLEDGEMENTS

Two anonymous reviewers provided insightful comments on the original manuscript. Eric Grissell and Michael Gates kindly helped us to access Schmieder's and Whiting's *Melittobia* vouchers at the National Museum of Natural History. This research was supported by NSF Grant 0088021, R. W. Matthews, principal investigator.

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