

Nesting biology, life cycle, and interactions between females of *Manuelia postica*, a solitary species of the Xylocopinae (Hymenoptera: Apidae)

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Abstract The Xylocopinae contains four tribes with species which show a range of nesting habits, from solitary to social. The Manuelliini is the sister group to all other Xylocopine tribes, with one genus, *Manuelia*, of three species found mainly in Chile. This is a solitary genus, whose biology is scarcely known for two species, *M. gayatina* and *M. gayi*, and so far completely unknown for *M. postica*. This paper reports on nesting substrates, nest architecture, nesting behaviours, life cycle, and interactions between females at nesting sites, for *M. postica*. The results indicate that *M. postica* presents some features which are typical of solitary life, and also some features which are unusual in solitary bees but have been reported in phylogenetically more apical social species. Our findings open interesting questions on the ecological scenarios involved in the evolution of sociality within the Xylocopinae.

Keywords *Manuelia postica*; nest architecture; nesting behaviour; solitary bee

INTRODUCTION

The Xylocopinae (Hymenoptera: Apidae) is currently hypothesised as the sister group to other Apidae subfamilies (Michener 2000). It has emerged as a valuable model to study transitions in social evolution (e.g., Schwarz et al. 1997, 1998, 2007; Tierney et al. 2002) because it contains species ranging from solitary to social in nesting behaviour and social organisation (Michener 2000). In the Xylocopinae, some solitary species exhibit features unusual in non-social life, which have been proposed as prerequisites for evolution to social life (Michener 1974, 2000). Several of such features are related to nesting biology: (a) protection of immature offspring through guarding behaviour by the mother, (b) physical contact between the mother and her developing offspring while she cleans their cells, (c) existence of hibernating assemblages enabling contact between siblings, and sometimes between siblings and their mother, and (d) tolerance between these nestmate individuals inside the nest (Michener 1969, 1974, 1985). Although such features are probably precursors to social life, none of them is sufficient for the development of sociality (Sakagami & Maeta 1977). To evaluate whether these behavioural characters are precursors of sociality in the Xylocopinae, information is needed on the nesting biology of non-social sister groups of eusocial taxa, which may enable phylogenetic comparative analyses aimed at reconstructing ancestral states of social life.

The Xylocopinae contains four tribes: Manuelliini, Xylocopini, Allodapini, and Ceratinini (Daly et al. 1987; Sakagami & Michener 1987). Nesting and social behaviour have been studied in several species of Xylocopini, Allodapini, and Ceratinini (reviews on Xylocopini: Gerling et al. 1989; Michener 1985, 1990; on Allodapini: Schwarz et al. 1997, 1998; on Ceratinini: Michener 1985, Sakagami & Maeta 1995). Manuelliini is a monogenerical tribe constituted by the genus *Manuelia* Vachal, which includes only three species: *M. postica*, *M. gayi*, and *M. gayatina* (Sakagami & Michener 1987) found mainly in Chile (Daly et al. 1987). *Manuelia* has been proposed

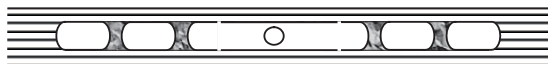


Fig. 1 Characteristics of nests of *Manuelia postica*: diagram of a nest containing an entrance hole, an entrance chamber, and four cells separated by partitions, two at each side of the chamber.

as a relict genus (Michener 1979; Daly et al. 1987), constituting a sister group to all other Xylocopinae (Sakagami & Michener 1987), and retaining several ancestral morphological features (Michener 2000). It thus represents an interesting taxon for the study of potential ancestral states of nesting biology. The only data published on the biology of the genus *Manuelia* refer to limited field observations and nest dissections of *M. gayi* and *M. gayatina* (Claude-Joseph 1926; Daly et al. 1987). In this paper we report on nesting substrates, nest architecture, nesting behaviours, life cycle, and interactions between females at nesting sites, for *M. postica*.

MATERIALS AND METHODS

Nesting and life cycle observations

All observations were made at Altos de Lircay National Park, east of Talca, Chile (35°29'S; 70°58'W), during yearly field campaigns starting in October (early spring) of one year and ending in April (mid autumn) of the next year, from 2001 until 2006. Eighteen observation periods were included in the most intensive campaign, from the third week of October 2005 to the last week of April 2006 (for exact dates, see Table 1). Nests were collected between 8:00 and 11:00 h. Prior to collection, nest entrances were blocked with Teflon tape affixed with masking tape. Twenty-five nests were collected in each period, and dissected in the field to permit observations on nesting behaviour, nest architecture, and life cycle.

Behaviours observed in nesting sites

During December 2005, presence or absence, and position (head or abdomen showing through the nest entrance) of *M. postica* females at the nest entrance were determined at 54 nests, examined in the field between 16:00 and 19:00 h. In a random sample of those nests ($N = 28$), the number and sex of adults inside the nests were recorded. Additionally, during

January 2006 the behaviours of females at or near the nest entrance were recorded in each of 10 nesting sites (with a mean of c. 5 nests per site) observed on separate days from 9:00 to 12:00 and from 16:00 to 19:00 h.

RESULTS

Nesting substrates

Most nests of *M. postica* were found in dead stems ($N = 810$) or in dry internodes of live stems ($N = 17$) of *Chusquea quila* (Poaceae: Bambuseae). Occasionally, nests were found in dead stems of *Aristotelia chilensis* (Elaeocarpaceae) ($N = 12$), and *Rubus ulmifolius* (Rosaceae) ($N = 15$). The nests in these three plant species were similar in the linearity of their structure, cell disposition, location and number of nest entrances, and position of cells with respect to the nest entrance. The detailed descriptions which follow refer to nests in *C. quila*.

Nest construction, architecture, and occupancy

Nest construction by females of *M. postica* began in early spring, and continued until late spring (Table 1). The nests consisted of a tunnel with cells arranged linearly along the plant stem, and separated by biconcave partitions made of wood particles (Fig. 1). Nests had one entrance in the middle portion of the tunnel. In nests dissected at the first and last observation periods ($N = 50$), distinct cells were not observed. Most nests during the other observation (breeding) periods had cells only at one side of the nest entrance (327 out of 400 dissected nests).

In the first observation period in early spring, most nests contained hibernating assemblages of F_0 individuals. Thereafter, no hibernating F_0 assemblages were seen. During the last observation period, nests contained hibernating F_1 assemblages. Adult females found inside nests in the intermediate period corresponded to the parental generation, F_0 . When females were present ($N = 221$ out of 400), the most frequent number of such females was one ($N = 196$), followed by two ($N = 23$), and three ($N = 2$). Larvae appeared in late spring. By mid summer most nests contained newly emerged adults, and hibernating F_1 assemblages were first detected. The proportion of nests containing F_1 hibernating assemblages increased steadily until the last observation period, and so did the number of adults present in them (Table 1).

Eggs								
Larvae								
Pupae								
Recently emerged females								
Young females								
Recently emerged males								
Young males								
Nests with hibernating groups								
	early	mid	late	early	mid	late	early	mid
	Spring			Summer			Autumn	

Fig. 2 Summary of the life cycle of *Manuelia postica*. Shaded areas show periods of occurrence of different life stages, based on data in Tables 2 and 3.

Life cycle and brief description of immature stages

The life cycle of *M. postica* is presented in Table 2 and summarised in Fig. 2. Food masses were semi-solid to solid, nearly rectangular, with the main axis along the tunnel, the side in contact with cell surface convex, and the opposite side flat. Eggs were found on the flat side of food masses, each with its main axis parallel to the main axis of the food mass. The shape of eggs was that of a slightly curved cylinder with convex ends, roughly 3 mm in length and 1 mm in diameter, whitish in colour but nearly transparent, and with a smooth and shiny chorion. First instar larvae were translucent, and they rested on top of nearly intact food masses. Pre-defaecating larvae were readily recognised because food masses had been modified, but there were no faeces visible. Post-defaecating larvae were identified because the food masses had been consumed and faeces were evident inside the cell. Larvae were considered as prepupae when they showed a marked increase in sclerotisation of the head capsule, the colour of the body cuticle had changed from bright white to opaque white, and a body constriction had developed between what would become the thorax and the abdomen. In general, larvae did not have tubercles, hairs or spicules, their bidentate mandibles had a concavity (as in *Ceratina* spp.), and they showed a basal tapering in the more slender apex (as in *Xylocopa* spp.), antennal papillae, and a small salivary opening (as in *Ceratina* spp. and *Xylocopa* spp.). Five consecutive types of pupae were easily identified on the basis of the colour of the eyes, the body, and the last abdominal segments. In general, pupae

showed a protuberance in the femur, and spines on the coxa, trochanter, and also on the second to the last abdominal tergum; this latter exhibits a strong medium acute projection (as in *Xylocopa* spp.). The newly emerged adults from the first generation were recognised by their whitish incompletely developed wings. Finally, young females and young males from the first generation were easily identified because they had fully developed wings and they were found inside their breeding cells.

Measurements and comparisons related to nest biology

Table 3 reports data obtained from nests analysed during the breeding period, some of which are used to compare *M. postica* with other bee species (see Discussion). Cells containing females were longer than cells containing males (ANOVA: $F_{1,69} = 83.77$; $P < 0.001$), but their diameters did not differ significantly (ANOVA: $F_{1,69} = 2.39$; $P > 0.1$). Wings were longer and intertegular distances greater in females than in males (ANOVA: $F_{1,88} = 189.65$, $P < 0.001$; $F_{1,88} = 161.35$; $P < 0.001$, respectively).

In a sample of 20 nests, differences in the number of cells in nests with one ($N = 10$) or two ($N = 10$) females were not significant (Mann-Whitney *U*-test: $Z = -1.22$, $P = 0.22$). Differences in the mean dry weight of food masses between nests with one ($N = 10$) or two ($N = 10$) females were not significant either (Mann-Whitney *U*-test: $Z = -0.48$, $P = 0.62$).

The number of adult individuals per nest (including hibernating nests found in the last observation period) was negatively correlated with mean wing length of individuals in each nest (Pearson

product-moment correlation: $N = 25$; $R = -0.50$; $P = 0.01$), and with mean intertegular distances of individuals in each nest (Pearson product-moment correlation: $N = 25$; $R = -0.62$; $P = 0.0008$). These data were used to assess a potential trade-off between the size and number of progeny.

Guarding behaviour

Observations of 54 nests monitored during part of the breeding period (December 2005) are summarised in Table 4. When females were present at the nest entrance, either their head (inspecting behaviour) or their abdomen (guarding behaviour) could be seen from the outside. When the nest was disturbed, such as by a movement of the stem, inspecting females turned around and blocked the nest entrance with the apical metasomal tergum, thus adopting a guarding posture. While most nests had a female at the

entrance, no males were ever found in such a position. Nests with only one female were more frequent than nests with two females (Table 4).

Interaction between females in nesting sites

During part of the breeding period (January 2006), 10 nesting sites (with a mean of c. 5 nests per site) were selected and each one of them was observed during one day from 9:00 to 12:00, and from 16:00 to 19:00 h. Altogether, 92 behavioural events were registered at the nest entrance, near the nest entrance, or towards the nest entrance (Table 5). The most frequent behaviour was a type of agonistic interaction at the nest entrance, consisting of the approach by an intruder female flying or walking with hovering movements, while the nest entrance was blocked by a guarding female, and the intruder subsequently touching and pushing the resident female.

Table 3 Data obtained from dissection of *Manuelia postica* nests in the field, during all observation periods between October 2005 and April 2006. Lengths (mm) and weights (mg) were determined in the laboratory.

Period	Parameter	<i>N</i>	Mean	Min.	Max.	SD
Breeding	Cell length (with brood)	95	9.03	7.2	10.2	0.62
	Cell diameter (with brood)	95	4.59	3.9	5.8	0.28
	Partition thickness	50	2.25	1.1	3.1	0.40
	Nest entrance diameter	30	2.88	2.8	3.0	0.04
Food mass provisioning	Cells/nest	20	3.05	2.0	5.0	0.83
	Food mass dry weight	61	4.23	4.0	4.4	0.11
Late breeding	Cell length (with female)	44	9.97	8.1	11.0	0.63
	Cell diameter (with female)	44	4.71	4.0	5.2	0.28
	Cell length (with male)	27	8.46	7.0	9.7	0.75
	Cell diameter (with male)	27	4.61	4.0	4.9	0.19
Aggregation of individuals, partitions destroyed	Tunnel length	25	66.17	40.8	141.7	24.22
	Tunnel diameter	25	4.39	4.1	4.8	0.16
	Individuals/nest	25	4.04	2.0	8.0	1.93
	Wing length, female	57	7.90	7.4	8.4	0.27
	Intertegular distance, female	57	2.11	1.9	2.4	0.13
	Wing length, male	33	7.05	6.2	7.6	0.30
	Intertegular distance, male	33	1.78	1.5	2.1	0.11

Table 4 Data from observation and dissection of *Manuelia postica* nests in the field. In parentheses, number of nests observed (total = 54). Number of nests dissected: a = 3, b = 15, c = 10.

	Type of nest		
	With inspecting female	With guarding female	Without female at entrance
Nests with one female	100% a	86.6% b	70% c
Nests with two females		13.3% b	10% c
Nests without females			20% c

Table 5 Behaviour of *Manuelia postica* females at or in the vicinity of the entrance of nests. The total number of behavioural events recorded was 92.

Site where behaviour was observed	Behaviour observed	% times observed
Towards nest entrance	Female walks straight towards nest without guarding female	1.4
	Female performs hovering walk towards nest with guarding female	4.1
	Female performs straight flight towards nest without guarding female	1.4
	Female performs hovering flight towards nest with guarding female	17.8
Near nest entrance	Intruder female displaces guarding female	6.9
	Frontal approach between intruder female and guarding female	2.7
	Pursuit of one female by another	1.4
	Aggression in flight between two females	2.7
At nest entrance	Female enters nest without guarding female	5.5
	Inspecting female extends her head out and displaces intruder female	4.1
	Intruder female antennates towards inspecting female, and moves away	2.7
	Intruder female pushes guarding female	21.9
	Intruder female touches guarding female with its legs	27.4

DISCUSSION

Nesting substrates and nest architecture

Xylocopinae species nest in dead wood, or branches of plants and trees, digging into stems, occupying hollow stems, or using pre-existing cavities (Gerling et al. 1989; Maeta et al. 1992; Steen & Schwarz 2000). Nests of *M. postica*, as for other species of Xylocopinae including *M. gayi* and *M. gayatina* (Claude-Joseph 1926), were found in dry stems.

Xylocopine bees construct two main types of nests: branched and linear (unbranched) (Gerling et al. 1989; Michener 1990). Linear nests with the entrance at one end of the tunnel have a single cell construction zone, thus making communal life, *sensu* Michener (1974), virtually impossible (Sakagami & Maeta 1995). Linear nests with the entrance in the middle of the tunnel have two cell construction zones; in them, both solitary and social nesting have been documented (Sakagami & Maeta 1995). Nests of *M. postica* were linear, and some contained cells at both sides of the nest entrance, suggesting incipient social nesting. Moreover, nests of *M. postica* have been observed with more than one female of the parental generation during the breeding period. Although these facts may be taken as indications of a certain degree of intrinsic sociality, nests with cohabiting females have been documented in other solitary species (Michener 1974). The cohabitation in a nest of two females of certain bee species can represent a temporary event or a long lasting situation (Sakagami & Maeta 1977), and be determined by ecological restrictions such as availability of

pollen or nest sites, and by genetic factors such as the degree of genetic relatedness between females (Hogendoorn & Leys 1993; Schwarz et al. 1998). Work in progress in our laboratory is oriented towards distinguishing between these two possibilities.

Cells containing young females were longer than those containing young males, consistent with the greater dimensions of females (wing length and intertegular distance) compared with males. Studies on other bee species (*Apis mellifera*, *Diadasina distincta*) have also demonstrated that individuals of the larger sex occupy cells of greater dimensions (Taber & Owens 1970; Martins et al. 1999), whereas in *Xylocopa abbreviata*, in which sexes do not differ in size there is no difference in size between male and female cells (Ramalho et al. 2004). These facts suggest that females of *M. postica* can build cells to a given length depending on the sex of individual which will develop inside that cell. This behavioural pattern requires: (i) that *M. postica* females can control the size of cells, as has been proposed for the queen and workers of *Apis mellifera* (Koeniger 1970; Pratt 1998), and (ii) they have an haplo-diploid sex determination system allowing control of the sex of the egg oviposited, as has been demonstrated broadly in Hymenoptera (Page et al. 2002; Normark 2003).

Finally, there was a negative correlation between the number of individuals found inside a nest and their mean size (estimated by wing length and intertegular distance). If females have a fixed amount of resources available for reproduction, then there is likely to be a trade-off between the number and

size of the progeny, as has been described for most studies of semelparous arthropods that exhibit no parental care (related to continuous food provisioning), as is the case of *M. postica* (review: Fox & Czesak 2000).

Life cycle and nesting behaviour

The data in Tables 1 and 2 suggest there is one generation of *M. postica* per year, as in some Xylocopine species of temperate regions (Gerling & Hermann 1978). The breeding period begins in late spring and ends in mid autumn, as in other Xylocopine species (Michener 1985). Hibernating assemblages of adults of both sexes may be found both in late summer and autumn and also in early spring, at the beginning of the breeding season.

The genus *Manuelia* is considered to be solitary at the time of nest construction and food provisioning (Michener 1985; 2000). This proposal was likely based on descriptions of nest biology of *M. gayi* and *M. gayatina* (Claude-Joseph 1926; Daly et al. 1987). According to our observations, *M. postica* exhibits many characteristics of solitary behaviour (*sensu* Michener 1969) during nest construction and provisioning. Immature individuals were always observed inside cells with intact partitions. This observation strongly suggests a lack of contact between the immature siblings, and also between them and their mother, as has been reported for many, but not all, Xylocopine species (Sakagami & Michener 1987; Maeta et al. 1992). Contact between siblings, as in some Xylocopine species in which the first adults to emerge destroy cell partitions and pass over the younger sibs in order to reach the entrance of the nest (Michener 1985; Sakagami & Maeta 1995), was not registered in *M. postica*. On the other hand, the pattern of cell construction, food mass provisioning, egg laying, cell closure, and sequential repetition of these activities, is typical of solitary bees (Michener 1974). Finally, when pupae reach the adult stage they remain inside their cells for some days before destroying the cell partitions. When all partitions are destroyed, adults constitute a hibernating assemblage, as in other Xylocopine species (Michener 1985).

Guarding behaviour

Females of *M. postica* at the nest entrance exhibit either guarding (92.3% of cases observed) or inspecting (7.7% of cases) postures. When the nest is disturbed by an intruder, the guarding females remain in their posture, thereby preventing the entry of the intruder. These behaviours are similar

to those of *Braunsapis hewitti*, an Allodapini species which is seen inspecting in 4.5% of cases and guarding in 93.5% of cases (Maeta et al. 1992), but different from *Ceratina*, whose females often turn around, face the intruder, and secrete an odoriferous substance from the mouth (Maeta et al. 1992). This type of defensive behaviour has not been observed in *Braunsapis hewitti* (Maeta et al. 1992) nor in *M. postica*.

Guarding behaviour as described in *M. postica* is widespread in the Xylocopinae, i.e., Ceratinini (Sakagami & Maeta 1977; Michener 1985; Maeta et al. 1992), Allodapini (Mason 1988; Maeta et al. 1992; Hogendoorn & Schwarz 1998; Steen & Schwarz 1998), and Xylocopini (Ramalho et al. 2004), and may reflect the retention of a primitive defence mechanism closely related to nest architecture, i.e., a single, narrow nest entrance allowing an effective blockading with the metasoma (Ramalho et al. 2004).

On the other hand, guarding behaviour has two important advantages in social nesting bees: (i) more extended foraging trips by a female while another one remains at the nest entrance and hence, higher accumulation of pollen loads, and (ii) defence against conspecific or heterospecific invaders (Hogendoorn & Velthuis 1993). In relation to the first advantage, a longer foraging time when nests are occupied by two or more females has been correlated with an increase in the number of cells constructed in some Xylocopine species (Sakagami & Maeta 1977; Michener 1985). In *M. postica*, neither the number of cells per nest nor the mean dry weight of food masses per cell differed between nests with one or two females. Therefore, it is likely that in those nests of *M. postica* with two females inside during the rearing period, there is no coordinated foraging and guarding as described in social nesting Xylocopine bees.

In relation to the second advantage, guarding behaviour suggests strong pressure from conspecific individuals, i.e., usurpers and robbers, and heterospecific ones, i.e., predators and parasites (Ramalho et al. 2004). In *M. postica*, only attempts by conspecific individuals to enter the nests were observed. On the other hand, we found progeny of the parasitoid, *Macrogotea gayi* (Hymenoptera: Ichneumonidae), inside nests of *M. postica* containing larvae and/or pupae, and have observed its oviposition behaviour: when a female of the parasitoid lands on *C. quila* stems, she walks around feeling the stem surface with her antennae before curving her abdomen, inserting her ovipositor through the nest wall, and

laying an egg directly inside a cell. Therefore, the guarding female cannot prevent parasitism, so this interaction does not favour the evolution of guarding behaviour, further suggesting that guarding behaviour in *M. postica* is mainly a defence against conspecifics.

Interaction between females

In other Xylocopine species, robber conspecific females approach cautiously, and turn away as soon as they find a resident female; nest usurper conspecific females make direct approaches, are not deterred by the presence of a resident female, and normally push her aside when present (Hogendoorn & Velthuis 1993). Some behavioural interactions observed between *M. postica* females at the nest entrance were similar to these. Thus, intruders showed cautious approaches or aggressive behaviours near or at the nest entrance. On the other hand, the presence of two (or three) females inside a nest suggests either that a resident female allowed the entry of an intruder female, or that these females remained together after hibernation (Stark et al. 1990; Hogendoorn & Velthuis 1993). Some of these cohabiting females displayed tolerant interactions (i.e., permitting passing; one or both females passing venter-to-venter in opposite directions). Taken together, these facts suggest nestmate discrimination ability in *M. postica*.

CONCLUSIONS

This paper describes field observations on the nest biology of *M. postica* and on interactions between females, and compares the data with those from phylogenetically related species. The main characteristics of *M. postica* are: (i) it is a univoltine species, (ii) it shows cell construction and food provisioning strategies typical of solitary bees, (iii) some nests allow two zones of cell construction, (iv) females can regulate cell size depending on the sex of the individual which will develop inside, (v) nests with two females are not more productive than nests with one, (vi) the number of individuals per nest correlated negatively with the size of those individuals, (vii) females do not have contact with their developing offspring, (viii) there is no contact between immature siblings, (ix) females defend their nest through guarding behaviour, and (x) hibernating assemblages occur after the breeding period. The observation that a female of a solitary bee shares her nest with one and occasionally two females opens some interesting questions, for instance: can

such females recognise nestmate conspecifics and discriminate non-nestmates? Do females found inside a nest during the breeding period show a high degree of relatedness? Under what ecological circumstances do two or more females of a solitary bee species share a nest? We are currently engaged in finding answers to these questions, which will contribute to our understanding of social evolution in the Apidae.

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