BEHAVIOR

Brood Provisioning and Colony Composition of a Malagasy Species of *Halterapis*: Implications for Social Evolution in the Allodapine Bees (Hymenoptera: Apidae: Xylocopinae)

MICHAEL P. SCHWARZ,[1] SIMON M. TIERNEY, JOHN ZAMMIT, P. MEG SCHWARZ, AND SUSAN FULLER

Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia

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ABSTRACT Although the biology of most genera of allodapine bees is relatively well known, there are only fragmentary data on one African species of a basal genus, *Halterapis*, and there have been no studies of this genus from Madagascar where it is most speciose. We present the first account of nesting and social biology of a Malagasy species in this genus, *Halterapis minuta* Brooks & Pauly, based on a sample of 23 nests This species has a unique form of brood provisioning, where a clutch of eggs is mass provisioned with a single, long cylindrical pollen mass, and larvae gradually eat their way along this food store. Most colonies contained more than one adult female, with generational overlap and very strong size-related ovarian differentiation among nestmates, indicating that the species is eusocial. Sex allocation was extremely female biased, and this is probably linked to reproductive skew within colonies. Our findings indicate that the lack of true sociality in the African species *Halterapis nigrinervis* (Cameron) is apomorphic and not linked to mass provisioning per se, although it may be linked to mass provisioning of individual eggs. The form of sociality in *H. minuta* emphasizes earlier findings that sociality is frequently very complex in allodapine bees and further indicates that extant members of the tribe Allodapini do not represent early steps in the origin of eusociality.

KEY WORDS sociality, mass provisioning, eusociality, phylogenetics, Madagascar

ALLODAPINE BEES EXHIBIT WIDE variation in social behavior, ranging from predominantly subsocial to highly eusocial. This range in social types, combined with broad variation in life history traits, makes them an ideal system for comparative studies of social evolution (Schwarz et al. 1998). Recent studies have begun developing DNA sequence-based phylogenies for use in inferring transitions in social and life history traits (Tierney et al. 2002, Bull et al. 2003, Schwarz et al. 2003, S.M.T. and M.P.S., unpublished data). An important outcome of these studies has been a shift away from two major allodapine paradigms, namely, that the most basal extant lineage in this tribe was a mass provisioner and that sociality had arisen among the extant lineages. These paradigms were based on evidence that African species of *Halterapis* were subsocial mass provisioners (Michener 1971), and on phylogenetic hypotheses based on morphological and brood provisioning characters. On the basis of these data, it was implied that *Halterapis* and its partially mass provisioning sister genus *Compsomelissa* formed the sister group to the remaining allodapine genera (Michener 1977a, Reyes 1998). However, molecular evidence shows that the tropical African and Malagasy genus *Macrogalea* is the most basal allodapine genus (Schwarz et al. 2003; S.M.T. and M.P.S., unpublished data), and recent studies of *Macrogalea* species from Tanzania (Tierney et al. 2002), Malawi (S. Thompson and M.P.S., unpublished data), and Madagascar (M.P.S. and P.M.S., unpublished data) show that sociality is well developed in that genus.

A more recent molecular phylogeny focusing on the African allodapines (S.M.T. and M.P.S., unpublished data) shows that the non-*Macrogalea* taxa form two highly supported monophyletic clades of 1) *Allodape* + *Braunsapis* and 2) *Halterapis* + (*Compsomelissa* + *Allodapula*). The grouping of genera in the latter clade is also contrary to the previous phylogenetic hypotheses (Michener 1977a, Reyes 1998), although reevaluation of morphological and brood provisioning strategies by S.M.T. and M.P.S. (unpublished data) support the monophyly of this clade. *Halterapis* also occurs in Madagascar and in the absence of males and larval specimens, Michener (1977b) placed some members of Malagasy *Halterapis* (known only from female specimens) within *Allodapula.* More recent discovery of male specimens of many species (Reyes and Michener 1992, Pauly et al. 2001) indicated that the Malagasy fauna should be placed entirely within *Halterapis.* Consequently, Madagascar has a very rich assemblage of *Halterapis*, with 17 described species (Pauly et al. 2001), compared with four or fewer species from Af-

[1] E-mail: Michael.Schwarz@flinders.edu.au.

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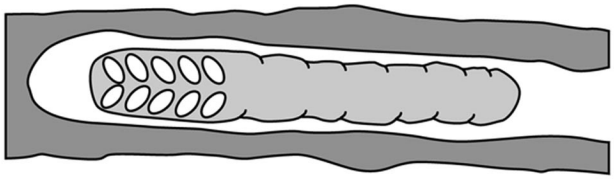

Fig. 1. Eggs and provision mass in rear end of nest. Note that eggs were underneath the provision and were not visible until the pollen had been removed, but they are shown in white here to indicate their position.

rica (Michener 1975). Given the paucity of research on Malagasy allodapines it is likely that the actual number of species will be much larger.

The only data on *Halterapis* species from Madagascar are based on flower-collected adults; their nesting biology, sociality, and immature morphology has thus far been completely unknown. In fact, even the biology of African species is poorly known. Michener (1971) described sociality for the genus based on 18 summer nests of two alternate forms of the *H. nigrinervis* group from three sites. These nests displayed only subsocial associations consisting of small multifemale assemblages of mothers joined by newly eclosed daughters, who were presumed to soon disperse, and there was no evidence for any form of cooperative brood rearing.

Based on Michener's African studies, *Halterapis* is the only allodapine genus that seemed to be entirely subsocial; all other nonparasitic genera for which data are available display some forms of sociality, involving semisocial, quasisocial, or eusocial grades of organization (Schwarz et al. 1998). Here, we describe the nesting biology and aspects of sociality in one Malagasy *Halterapis* species, *H. minuta* Brooks & Pauly, and we use these data to explore implications for broader aspects of social evolution within the Allodapini.

Materials and Methods

Nests were collected ≈5 km south of Anakao, a small fishing village ≈40 km south of Toliara (Tulear). The vegetation at our study site was low, open spiny forest interspersed with zebu and goat corrals. This region is arid and rainfall is mostly restricted to brief sporadic periods in January and February (mid to late summer), approximately corresponding to the time of our collection. Colonies were collected over a 5-d period from nests found in several large bushes of an unidentified genus that closely resembles the brooms (*Genista* and *Cytisus* spp.) in general appearance. It was not possible to collect nests outside of the expected bee foraging period (remoteness of bee sites with access only via walking tracks precluded dawn and dusk sampling); therefore, it is likely that some colony members were engaged in extranidal activity during nest collection. Nest entrances were sealed in situ with adhesive tape, and the nests were kept cool until opening. All nest occupants were preserved in either 100% ethanol for DNA analyses or in Kahle's solution for dissection.

Adult females were dissected in 70% ethanol by using the techniques of Schwarz (1986). The summed lengths of the three largest terminal oocytes were used as a measure of ovary size. Wing length (from the base of the wing to the apex of the submarginal cell) was used as a measure of body size. Wing wear was measured as the number of nicks and tears on the distal margins of the forewings and was used as a measure of activity and age. Insemination status was assessed by opacity of the spermatheca, but because of the minute size of these bees, spermathecae were often difficult to find, especially for uninseminated females where the spermatheca is completely transparent. Spermathecae were most easily located in reproductively active females where their opacity contrasted with surrounding tissues and in callow females where they occurred very close to the common oviduct.

Results

Nest Structure and Brood Provisioning. Nests were simple, unbranched cylindrical tunnels ranging from 14 to 79 mm in length and 2.3 mm in diameter. Entrances were either at the broken end of a dead stem or from the side of an unbroken stem. Collars were constructed at the entrance, evident by the often lighter and fibrous appearance of the collar compared with the surrounding material or the walls of the nest lumen, and they were ≈1.3 mm in diameter. It was apparent that in at least some cases, nests used a preexisting burrow made by some other insect. Such nests had secondary entrances, tunnels, or tunnel bases blocked off by packed plant fibers, modifying preexisting burrow dimensions to those of more normal nests.

H. minuta has a method of brood provisioning that is unique among allodapines studied to date. Of the 23 colonies collected, seven contained eggs, and in these nests the eggs were glued to one side of the nest lumen in an oval patch or in a chevron pattern. A single and slightly flattened large cylindrical mass of pollen mixed with nectar is placed directly over the eggs and continues up the nest column. An example of eggs and provision mass is illustrated in Fig. 1. In nests containing young feeding-stage larvae, it was clear that larvae gradually eat their way as a group up the pollen mass toward the nest entrance. Adults do not have access to larvae at this stage (because of the diameter of cylindrical pollen mass), so larvae must be able to move up the nest lumen unassisted as they eat. Larval mobility

Table 1. Colony contents and mean number of each developmental stage in our samples

Nest no.	Adult females	Adult males	Callow females	Eggs	Small larvae	Medium larvae	Large larvae and prepupae	Pupae
1	1							
2	1							
3	1					1		
4	1					1	2	
5	1		1				1	
6	1		1	3				
7	1		2		2	1		1
8	2							
9	3						2	
10	3			5			1	1
11	3		2	3	2			4
12	3		4				4	4
13	3		4				4	
14	3		5	8		1	6	3
15	4			6			3	
16	4		3				5	4
17	4		5				3	
18	5	3	1	1	1		6	
19	5		2		1		5	3
20	5		2		3	2	7	
21	5		3				5	5
22	6		1	11				1
23	6	7	1				4	
Mean	3.09	0.44	1.61	2.09	0.39	0.26	2.52	1.13

may be enabled by the long setae projecting from each of the two lateral thoracic tubercles. Older fourth instars were often found either with no food or with small individual pollen masses, and it was not clear whether these small masses were remnants of an original cylindrical mass or provided later in their development by adults. This form of provisioning is most similar to that found in *Allodapula,* where up to four immatures feed from a central communal food mass that is occasionally replenished by adults. Larvae of both genera also possess enlarged first two lateral tubercles (Skaife 1953; Michener 1971, 1976; S.M.T. and M.P.S., unpublished data).

Colony Composition and Phenology. The number of eggs, small-to-medium larvae, large larvae, prepupae, pupae, and callows for each nest, and mean values over all nests, are given in Table 1. Because our data are from a single time of year only, it is impossible to describe any seasonal patterns that might occur, although the following features are evident in our sample. 1) Most nests contained a broad range in developmental stages and the range of these stages did not seem to be correlated with the number of adult females. However, when eggs were present they always occurred as a single clutch, glued onto a small region of the nest near the terminal end of burrow. 2) The majority of nests contained callow females and just over half of these nests contained eggs, and small- or medium-sized larvae, indicating that these callows had the potential to provide substantial alloparental care, either in the form of providing food or defending brood against potential enemies.

Other studies on a number of allodapine species have examined brood number and per capita brood production (total number of immature brood/number of adult females) as a function of the number of adults females sharing a nest, and this measure has been used to infer the likelihood of benefits for group living. Visual inspection of scattergrams of total brood number against the number of fully pigmented adults and against number of callow adults suggested linear relationships. A multiple regression showed that total brood size increased with the number of noncallow adults ($b = 1.974$, $P < 0.001$), but the number of callows had no significant effect ($b = 0.707$, $P = 0.129$). The relationship between the number of noncallow females and total brood (Fig. 2) indicates that if there are only one or two reproductive females in each nest (see below), the number of brood produced is influenced by the potential number of helpers. Visual inspection of scattergrams suggested that any relationships between per capita brood production and either the number of females or number of callows was nonlinear, but analysis of variance (ANOVA) indicated no significant effect of either ($P > 0.28$ for both analyses). This contrasts with studies on Australian allodapines (Schwarz et al. 1998) and suggests that

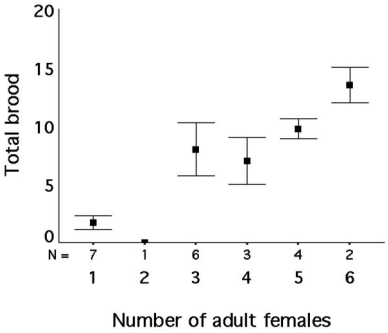

Fig. 2. Mean number of brood per nest (±1 SE) as a function of the number of noncallow nestmates. Samples sizes are given immediately below the abscissa.

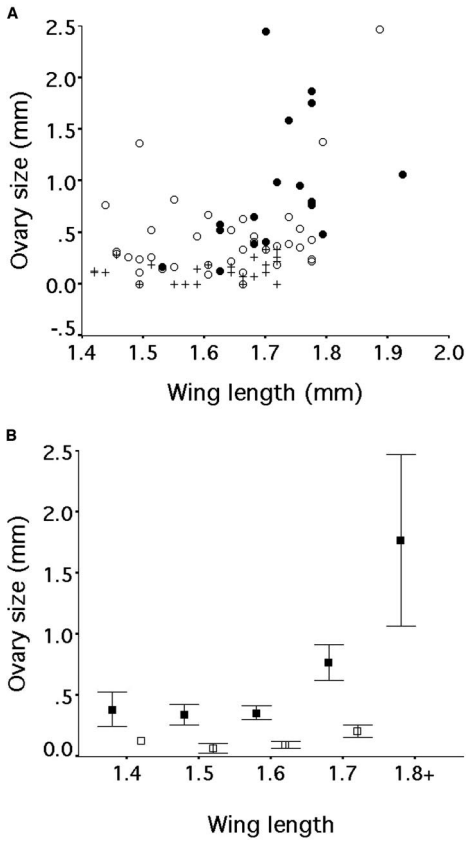

Fig. 3. (Top) Scattergram of ovary size against wing length for females from multifemale nests. Black circles represent noncallow females with wing wear, hollow circles represent noncallow females without wing wear, and crosses represent callows. (Bottom) Mean ovary size (±1 SE) for callow females (hollow squares) and noncallow females (black squares) from multifemale colonies.

increasing the number of females increases the number of brood, but it does not enhance per capita colony efficiency.

Reproductive Differentiation. The numbers of adult females per nest in our sample are shown in Table 1. Mean colony size was 3.09 noncallow females per nest, and the mean number of callows was 1.61. It is possible that noncallow females may have recently emerged, and this is discussed further below.

In Fig. 3, top, we plot ovary size against wing length for females from multifemale nests, where different plot symbols are used to indicate callows and noncallow females with worn and unworn wings. In Fig. 3, bottom, these data are summarized as mean values (calculated separately for callow and noncallow females) for wing length categories to reveal broader trends. No callows in our sample had any wing wear, and for those females where spermathecae were located ($n = 17$), none were inseminated. Several trends are evident from these graphs. First, callows had very small ovaries (in some cases without distinguishable oocytes). Second, females with wing wear tended to have larger mean ovary size than unworn noncallow females. Third, there seems to be a positive but nonlinear relationship between wing length and ovary size, such that the largest females have disproportionately large ovaries. Last, callows tended to have smaller mean wing length than noncallow females.

We further explored these patterns statistically. A Kruskal–Wallis nonparametric ANOVA indicated significant nest effects on wing length ($\chi^2_{16} = 42.96$, $P < 0.001$), a pattern that was clearly evident when dissecting females. When exploring the relationship between wing length and callow status while simultaneously taking nest effects into account, it was not possible to transform wing lengths to achieve homoscedasticity. We therefore calculated mean wing lengths for callow and noncallow females for each nest and compared these using a paired *t*-test. This test was highly significant ($t_{11} = 3.243$, $P = 0.008$), with callow females having shorter mean wing length.

Small ovary size and lack of wing wear are expected for callows and need not indicate that reproductive differentiation reflects any factor other than age. In addition, the relationship between ovary size and wing length could be due to body size scaling effects, i.e., larger females could have proportionally larger ovaries. We therefore carried out an ANOVA by using only noncallow females, with a body size-corrected ovarian index (ovary size/wing length) as the dependent variable, and with nest source as a random treatment and wing length as a covariate. Data were $\log_{10}(x + 0.1)$ transformed to achieve homoscedasticity. The interaction effect between wing length and nest source was nonsignificant ($F_{12, 27} = 0.952$; $P = 0.514$) and when the interaction term was removed, we found a nonsignificant effect of nest source ($F_{16, 39} = 1.360$; $P = 0.212$) but a highly significant effect of wing length ($F_{1, 39} = 17.773$; $P < 0.001$). We repeated the analyses by using raw ovary size rather than ovarian index, and this again indicated no interaction between nest source and wing length ($F_{12, 27} = 0.907$; $P = 0.552$), no effect of nest ($F_{16, 39} = 1.337$; $P = 0.225$) but a strong effect of wing length ($F_{1, 39} = 21.188$; $P < 0.001$). Together, the two sets of analyses indicate that body size influences ovarian size independent of scaling effects.

Last, we examined the relationship between wing wear and wing length. Wing wear tended to be small for these minute bees, a common finding in other studies on very small Hymenoptera. We categorized noncallow females as having either no or some wing wear (0 or 1+ wing nicks or tears) and then calculated mean wing length and mean ovary size for each of these groups for each nest. This left us with nine nests containing at least one worn and one unworn female. These mean values were then compared using paired *t*-tests, which indicated that worn females were both significantly larger in both body size ($t_8 = 3.020$, $P = 0.017$) and ovary size ($t_8 = 2.998$, $P = 0.017$) than their unworn nestmates. The distribution of wing lengths for callow females and for worn and unworn noncallow females from multifemale nests is summarized in Fig. 4, which indicates that callow and unworn adult

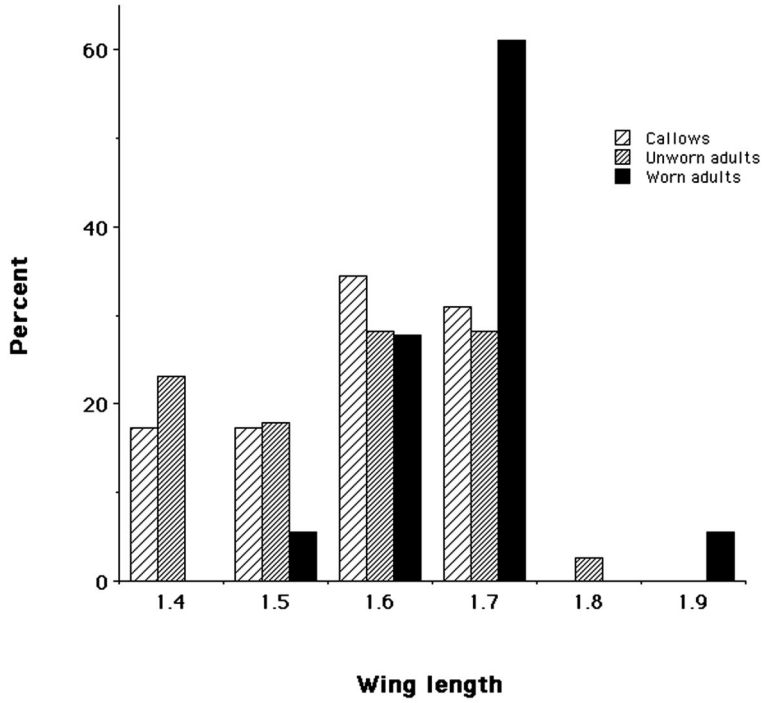

Fig. 4. Size distribution of callows, unworn adults (with full coloration), and worn adults as a function of wing length. Wing length was categorized into intervals of 0.1 mm.

females had a highly similar distribution of wing length, but that worn adults had a size distribution that was distinct. This suggests that unworn adult females could be from the same developmental or size cohort as the callows, but they were old enough to have developed full coloration. This also would be consistent with the slightly larger ovary sizes of adult unworn females, although it is clear that some unworn adult also had enlarged ovaries.

Sex Allocation. We investigated sex ratios based on pupae and callows in our sample. Of 26 pupae from nine nests, none were male, and of 37 callows from 15 nests, there also were no males. Ten fully pigmented adult males were found in our samples, and these came from two nests, one containing three males and the other containing seven. These data suggest that at the time of our samples male production is negligible but that some males had been produced earlier.

Discussion

Our data are from a single sample of nests at one time of the year, and this limits the kinds of conclusions that can be drawn regarding the life cycle of this species. However, they provide the first account of social biology in a Malagasy *Halterapis* species and are based on a larger sample of nests than for the only other species of *Halterapis* (from Africa) studied to date. Results presented here allow some aspects of social and nesting biology, important for understanding more general social evolution in allodapines, to be inferred.

To place our findings on *H. minuta* into a phylogenetic framework, we present a phylogeny containing three Madagascan *Halterapis* species, including *H. minuta,* and representatives from most nonparasitic genera. The phylogeny (Fig. 5) is based on Bayesian analysis of 2,477 nucleotides by using the techniques described in Schwarz et al. (2004) and a comprehensive study will be published elsewhere. This phylogeny suggests that current generic assignments may need to be revised, but for the discussion below it is important to note that the Madagascan *Halterapis* species are basal to the African species *H. nigrinervis* and that node support for this is strong.

Oviposition and Brood Provisioning Traits. The African species *H. nigrinervis* is unique among allodapines in that it completely mass provisions each egg shortly after each oviposition act. This had been thought to represent the plesiomorphic state for allodapines, with partial progressive provisioning of the *Compsomelissa* genus being apomorphic, and with full progressive provisioning being synapomorphic for the remaining allodapine genera. However, recent molecular phylogenetic studies (Schwarz et al. 2003, S.M.T. and M.P.S., unpublished data) indicate that mass provisioning in *Halterapis* is a derived trait, and the phylogeny in Fig. 5 confirms this. S.M.T. and M.P.S. (unpublished data) point out that provisioning of first instars with communal pollen masses for *Allodapula* (belonging to the same clade as the African *Halterapis*) suggests that mass provisioning in *Halterapis* may be simply a more extreme form of partial mass provisioning present in other groups. Current results show

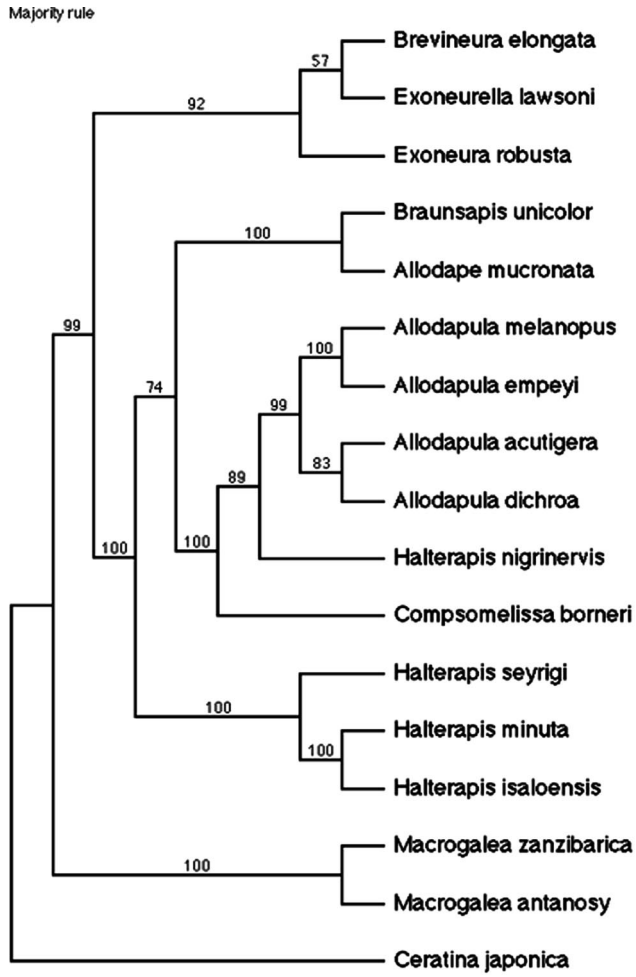

Fig. 5. Phylogeny of representatives of the major allodapine genera, including one *Halterapis* species from Africa (*H. nigrinervis*) and three from Madagascar (*H. seyrigi* Benoist, *H. minuta*, and *H. isaloensis* Brooks & Pauly). The phylogeny is a consensus phylogram based on a partitioned Bayesian analysis of cytochrome oxidase I (COI), cytochrome b (Cyt b), and the F2 copy of EF-1α, comprising 1,280, 427, and 770 nucleotides, respectively. Sequencing methods, partition models, and Bayesian techniques are given in Schwarz et al. (2004). Node support values are calculated as posterior probabilities from 5,000 trees, sampled every 500th generation after a burn in of 1.5 million generations.

that *H. minuta* also mass provisions their eggs, but in a unique manner, whereby a clutch of eggs share a communal mass provision. This communal provisioning is begun after oviposition of the clutch and can continue after larval eclosion. In *H. minuta,* the larvae gradually eat their way up the nest lumen as a group, showing some similarity to African species of *Allodapula* where larvae occur in a parallel contiguous group, venter to venter, with communal food being progressively replenished to their shared anterior feeding region. *H. minuta* therefore shares characteristics of African species of both *Allodapula* and *Halterapis.* At the same time, the unique method of provisioning in *H. minuta* further extends the range of provisioning strategies in allodapines. Indeed, combined with previous studies of other allodapine taxa, our results indicate that the tribe Allodapini displays the most diverse range of provisioning strategies of any extant bee group, a feature that is paralleled by the extreme diversity in larval morphology, which is greater than that of all other bees combined (Michener 1977, 2000). Significantly, this tribal radiation coincides with both the loss of cells and the transition from mass to progressive rearing.

The method of provisioning in *H. minuta* also has implications for social behavior. Food is provided to eggs after oviposition has been completed, and the large communal food mass cuts off contact between adults and brood. This means that if more than one egg layer occurs in a colony at a time, then once provisioning begins it is not possible for females to direct food resources to their own larvae. Furthermore, mass provisioning of a group of eggs will require that reproductive output in a colony is episodic, creating the potential for a female to monopolize reproduction before commencement of mass provisioning. Indeed,

dissection data strongly suggest that each colony had one reproductively dominant female at the time of collection.

Social Behavior. Our dissection and nest contents data indicate that during oviposition most colonies comprise one or more older females and a group of recently emerged females. Dissection data suggest that before oviposition, only one female had enlarged ovaries, and data from nests with recently laid eggs suggest that only one female had contributed either mostly or entirely to egg production.

One very interesting and clear pattern to emerge from our data is that reproductively active females tend to have larger body size than their nestmates and the population as a whole. In some cases, the reproductively dominant female had substantially larger body size than her nestmates, and during dissection it was usually easy to predict which female was reproductively dominant from body size alone. These females tended to have at least some wing wear and in our sample only one female was found who had large body and ovary sizes but lacked wing wear. Mean body size of callows was significantly smaller than for adult females, and among adult females, those with worn wings and large ovaries had significantly larger body size than their unworn nestmates. Although ovary size was greater for larger sized females, this was not due to body size scaling effects. These patterns strongly suggest the existence of a size-based reproductive caste system where younger females belong to a size group that is strongly underrepresented among reproductively active females.

The relationship between body size and reproductivity is stronger than for nearly all other allodapines where this has been investigated and is matched only by the Australian species *Brevineura xanthoclypeata* (Rayment) (Tierney et al. 1997) and the highly eusocial *Exoneurella tridentata* (Houston) (Houston 1977, Hurst 2002). Because such size-related ovarian differentiation does not occur in other members of these three genera, and reproductive castes are absent in the most basal allodapine genus *Macrogalea* (Tierney et al. 2002; S. Thompson and M.P.S., unpublished data; M.P.S. and P.M.S., unpublished data), it is apparent that a strong relationship between body size and reproductive differentiation has evolved at least three times in the Allodapini. The evolution of such size based reproductive castes also has arisen multiple times in other Hymenoptera, including halictine bees (Danforth 2003), corbiculate bees (Engel 2001), sphecid wasps (Matthews 1991), vespid wasps (Carpenter 1991), and ants. The identification of these independent origins, spread across diverse families and based on well-supported phylogenies, creates the opportunity for very broad comparative approaches to the evolution of advanced forms of eusociality.

The existence of a largely nonreproductive group of small body-sized females in *H. minuta* coincides with our data indicating that sex allocation is very strongly female biased. Of 63 pupae and callows, none were male, and of 71 noncallow adults, only 10 were males and these came from only two nests. The existence of strong female bias in this species is further supported by collections of adults from flowers by Pauly et al. (2001), comprising 113 females and no males. A low proportion of males would be expected if a substantial proportion of females in the population were nonreproductive, which is suggested by our dissection data.

Implications for Understanding Social Evolution in Allodapines. Before very recent molecular phylogenetic work, it was thought that solitary behavior was the ancestral state for the allodapines, because of solitary nesting in African *Halterapis* species, and because morphology-based arguments suggested that *Halterapis* was the sister group to the remaining allodapine genera. The latter conjecture has now been shown incorrect (Schwarz et al. 2003; S.M.T. and M.P.S., unpublished data) and that in fact solitary nesting in African *Halterapis* is apomorphic. Our findings indicate that solitary nesting is not synapomorphic for all *Halterapis* species. Small samples of several other Malagasy *Halterapis* species that we obtained during this study also show strong indications of size-based castes (M.P.S., unpublished data). Solitary nesting in African *Halterapis* coincides with mass provisioning, and although *H. minuta* is also a mass provisioner, food is provided for clutches rather than individual eggs. This suggests that solitary nesting in the African species *Halterapis nigrinervis* is associated not with mass provisioning per se, but rather associated with sequential mass provisioning of individual brood. Exploration of this possibility must wait until further data are obtained on Malagasy *Halterapis* species where, based on very small samples (M.P.S., unpublished data), provisioning strategies are likely to vary.

Schwarz et al. (2003) pointed out that although mass provisioning in African *Halterapis* species may seem unique, eggs and larvae in the closely related clade of *Allodapula* are provided with shared partial provisions, and eggs are laid in clutches. Molecular evidence and reevaluation of morphological traits (S.M.T. and M.P.S., unpublished data) show that these two African genera are more closely affiliated than previously thought, and life history traits detailed in this study show *H. minuta* seems to combine characteristics of both these taxa, namely, a mass provision that is shared by a clutch of eggs. Because sociality varies among these three groups, it may be possible to identify the relationship between provisioning strategies and sociality, but a well-resolved phylogeny covering a broad range of Malagasy *Halterapis* will be required.

Although allodapines have often been regarded as representing early stages in the evolution of sociality (Wilson 1971; Michener 1974, 1985, 1990), recent sequence-based phylogenetic studies indicate that extant lineages have a very long social history going back to at least the origin of the tribe (Tierney et al. 2002, Schwarz et al. 2003). Our results presented here add further support to the notion that well developed forms of sociality were in place before sequential mass provisioning of eggs and solitary behavior evolved in the African *Halterapis* species.

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References Cited

Bull, N. J., M. P. Schwarz, and S.J.B. Cooper. 2003. Phylogenetic divergence of the Australian allodapine bees (Hymenoptera: Apidae). Mol. Phylogenet. Evol. 27: 212–222.

Carpenter, J. M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae, pp. 7–32. *In* G. K. Ross and R. W. Matthews [eds.], The social biology of wasps. Cornell University Press, Ithaca, NY.

Danforth, B. N. 2003. Evolution of sociality in a primitively social lineage of bees. Proc. Natl. Acad. Sci. U.S.A. 99: 286–290.

Engel, M. S. 2001. Monophyly and extensive extinction of advanced eusocial bees: insights from an unexpected Eocene diversity. Proc. Natl. Acad. Sci. U.S.A. 98: 1661–1664.

Houston, T. F. 1977. Nesting biology of three allodapine bees in the subgenus *Exoneurella* Michener. Trans. R. Soc. S. Aust. 101: 99–113.

Hurst, P. S. 2002. Social biology of *Exoneurella tridentata,* an Australian allodapine bee with morphological castes and perennial colonies. Ph.D. thesis, School of Biological Sciences, Flinders University, Adelaide, Australia.

Matthews, R. W. 1991. Evolution of social behavior in sphecid wasps, pp. 570–602. *In* G. K. Ross and R. W. Matthews [eds.], The social biology of wasps. Cornell University Press, Ithaca, NY.

Michener, C. D. 1971. Biologies of the African allodapine bees. Bull. Am. Mus. Nat. Hist. 145: 223–301.

Michener, C. D. 1974. The social behavior of the bees. Harvard University Press, Cambridge, MA.

Michener, C. D. 1975. A taxonomic study of African allodapine bees. Bull. Am. Mus. Nat. Hist. 155: 67–240.

Michener, C. D. 1976. Larvae of African allodapine bees. 4. Halterapis, *Compsomelissa, Macrogalea,* and a key to African genera. J. Entomol. Soc. S. Afr. 39: 33–37.

Michener, C. D. 1977a. Discordant evolution and the classification of allodapine bees. Syst. Zool. 26: 32–56.

Michener, C. D. 1977b. Allodapine bees of Madagascar. Am. Mus. Novitates 2622: 1–18.

Michener, C. D. 1985. From solitary to eusocial: need there be a series of intervening species?, pp. 293–305. *In* B. Holldobler and M. Lindauer [eds.], Experimental behavioral ecology. Gustav Fischer Verlag, Stuttgart, Germany.

Michener, C. D. 1990. Castes in xylocopine bees, pp. 123–146. *In* W. Engels [ed.], Social insects: an evolutionary approach to castes and reproduction. Springer, Berlin, Germany.

Michener, C. D. 2000. The bees of the world. John Hopkins University Press, Baltimore, MD

Pauly, A., R. W. Brooks, L. A. Nilsson, Y. A. Persenko, C. D. Eardley, M. Terzo, T. Griswold, M. Schwarz, S. Patiny, J. Munzinger, et al.. 2001. Hymenoptera Apoidea de Madagascar. Ann. Zool. Wetenschappen 128: 1–390.

Reyes, S. G. 1998. A cladistic analysis of the bee tribe Allodapini. Philip. Entomol. 12: 55–84.

Reyes, S. G., and C. D. Michener 1992. The genus *Halterapis* Michener 1969 in Madagascar. Trop. Zool. 5: 249–253.

Schwarz, M. P. 1986. Persistent multi-female nests in Australian allodapine bee, *Exoneura bicolor.* Insect Soc. 33: 346–348.

Schwarz, M. P., N. J. Bull, and K. Hogendoorn. 1998. Evolution of sociality in the allodapine bees: a review of sex allocation, ecology and evolution. Insect Soc. 45: 349–368.

Schwarz, M. P., N. J. Bull, and S.J.B. Cooper. 2003. The molecular phylogenetics of allodapine bees, with implications for the evolution of sociality and progressive rearing. Syst. Biol. 52: 1–14.

Schwarz, M. P., S. M. Tierney, N. J. Bull, and S.J.B. Cooper. 2004. Molecular phylogenetics of the allodapine bee genus *Braunsapis:* A-T bias and heterogeneous substitution parameters. Mol. Phylogenet. Evol. 32: 110–122.

Skaife, S. H. 1953. Subsocial bees of the genus *Allodape.* J. Entomol. Soc. S. Afr. 16: 1–16.

Tierney, S. M., M. P. Schwarz, and M. Adams 1997. Social behavior in an Australian allodapine bee *Exoneura* (*Brevineura*) *xanthoclypeata.* Aust. J. Zool. 45: 385–398.

Tierney, S. M., M. P. Schwarz, T. Neville, and P. M. Schwarz. 2002. Sociality in the phylogenetically basal allodapine bee genus *Macrogalea* (Apidae: Xylocopinae): implications for social evolution in the tribe Allodapini. Biol. J. Linn. Soc. 76: 211–224.

Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge, MA.

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