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Biology of a nocturnal bee, *Megalopta atra* (Hymenoptera: Halictidae; Augochlorini), from the Panamanian highlands

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Bees of the genus *Megalopta* have gained attention as a result of their social nesting and nocturnal foraging. Seventeen nests of *Megalopta atra* from the highlands of Chiriqui Province, Panama, were collected at the end of the dry season when brood rearing is expected to be at its peak. Most nests contained single females; within multifemale nests only one female possessed enlarged ovarioles, although some non-reproductive individuals were inseminated. In two of these nests reproductive individuals were clearly larger in body size than nestmates, but body size variation and macrocephaly were equivalent to those found in other Neotropical augochlorines. There was no evidence of a non-reproductive worker-like caste and multifemale nests did not appear to be more productive than solitary nests, which may represent pre-reproductive assemblages. *Megalopta atra* appears to be isolated by altitude from co-genera common in Panama, this is discussed in comparison with temperate halictine bees, in which environmental clines separate solitary from social populations.

Keywords: Augochlorini; *Megalopta*; nesting biology; nocturnal bees; social evolution

Introduction

The halictine sweat bees are viewed as one of the most useful groups for investigations into the origins of social behaviour, largely because of the plasticity in degrees of social organization enabled by facultative caste systems, but also because of the numbers and diversity of species and the range of habitats occupied by these bees (Michener 1974, 1990; Danforth and Eickwort 1997; Wcislo 1997; Yanega 1997). Extrinsic factors are increasingly thought to play a role in shaping the kinds of social behaviour expressed, and the trend for temperate social taxa to largely revert to solitary living at higher altitudes and latitudes is often cited in support of this claim (e.g., Sakagami and Munukata 1972; Packer 1990; Eickwort et al. 1996; Soucy 2002; but see Soucy and Danforth 2002).

Transitions of species into novel environments are therefore of interest in understanding behavioural transitions (e.g., Wcislo 1989; West-Eberhard 2003). One other such example is movement into a nocturnal environment, and recently the augochlorine genus *Megalopta* has attracted the attention of biologists for exactly this reason (Arneson and Wcislo 2003; Smith et al. 2003, 2007, 2008; Wcislo et al. 2004; Kelber et al. 2006; Wcislo and Gonzalez 2006). Very little is known of the

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biology of the stem-nesting *Megalopta* outside of Barro Colorado Island (BCI), Panama. Here we detail the nesting biology of *Megalopta atra* Engel from the western Panamanian highlands, as part of comparative biological and phylogenetic studies of the genus.

Material and methods

Fieldwork was conducted at Reserva Forestal Fortuna, situated in western Panama at the border of Chiriqui and Bocas del Toro Provinces. The area is a mountainous region formed by the Serranía del Tabasará and the Cordillera de Talamanca that continues west into Costa Rica (see Myers 1969). These east–west ridges form the continental divide with unbroken highlands up to the ~1200-m contour in Panama, and isolated peaks up to 3475 m (Volcán Barú). The mountain range slopes north to the Atlantic lowlands, and south through foothills to the Pacific Ocean. The highlands contain montane rain forest or cloud forest, except on the higher peaks, with premontane moist or wet forest at lower elevations, though extensive areas have been cleared for cattle ranching and farming. Temperatures are cool and equable. A dry season usually lasts from approximately February to April, although rain falls in all months, with about 4000–5000 mm of rain per year, and the intensity of the dry season varies greatly from year to year (see www.stri.org/english/research/facilities/terrestrial/fortuna/research_info.php). Low clouds and light mist are common.

Research was based out of the Fortuna field station of the Smithsonian Tropical Research Institute (STRI; 8°43'N, 82° 14'W; ~1235 m elevation). Collections were made towards the end of the dry season – 24 April to 1 May 2007. Nests were collected and sealed in the field, and were later opened in the laboratory. Adults were preserved in absolute ethanol and brood cells were removed intact and housed in cell culture trays to rear as many adults as possible. Flying bees were collected using mercury vapour light traps situated at the STRI field station and at three locations of varying altitude down the Caribbean slope of the divide (~1160 m, 1010 m and 664 m).

Reproductive activity of adult females was inferred by dissection following Schwarz (1986). Ovarian development was measured as the sum length of the three largest terminal oocytes and mating status was identified by the presence or absence of sperm in the spermatheca. Body size was determined by intertegular distance, following Tierney et al. (2008). The number of nicks and tears along the distal margin of this wing was taken as a measure of wing wear. Voucher specimens are deposited in the Dry Reference Collection of the Smithsonian Tropical Research Institute, Balboa, Ancón, Panama.

Results

Seventeen *M. atra* nests were collected (Table 1). Nest and brood cell architecture did not differ from that described for other Panamanian species of *Megalopta* (Wcislo et al. 2004). Nest lengths ranged from 47 to 372 mm and nest tunnel width varied from 8 to 14 mm. While there was no evidence to suggest that nests with multiple females were longer than the nests of single females, the largest nest in this study, containing eight females (nest 13), did have a larger tunnel width and was in a stem of much broader diameter that contained two parallel sets of tunnels.

Table 1. *Megalopta atra* nest census data.

Nest number	Nest length (mm)	Tunnel width (mm)	<i>n</i> adult females	<i>n</i> sealed cells (brood)	<i>n</i> cells being provisioned with pollen	<i>n</i> total brood cells
1	47	–	1	2	1	3
2	271	11	1	0	1	1
3	372	9	1	2		3
4	96	8	0	3		3
6*	275	11	2	0	1	11
7	68	9	1	2		2
8	–	–	1	2	1	3
9	237	9	1	5		5
10	190	11	1 dead	0		3
11	132	12	0	1		6
12*	135	10	2	1		3
13*	242	14	8	7		8
14	119	8	1	0	1	1
15	195	11	1	1	1	3
16	156	11	1	0		2
17	230	9	1	3	1	4
18	223	9	0	0		1
Mean	186.8	10.1	1.4	1.7	0.4	3.6
±SE	21.5	0.4	0.4	0.5	0.1	0.6

Data show physical nest properties and the numbers of adults and brood.

*Multifemale nest.

Three nests were abandoned but contained brood cells. Eleven nests contained single females (one deceased) and three were multifemale; two nests contained two females each and one nest had eight females. All nests contained brood cells: the nests of single females contained one to five cells and the nests with multiple females contained three to eight cells. A better indication of colony productivity at the time of nest collection is the number of cells sealed or being provisioned: for singletons this ranged from zero to five cells and for multifemale nests it ranged from one to seven cells. Based on relatively small sample sizes, it does not appear that group nesting results in increased productivity on a *per capita* basis.

There is considerable intraspecific variation in female body size (range of intertegular width=2.56–3.76 mm), including enlarged processes of the head and genal spines, as known for some other Neotropical, social augochlorine bees (reviewed in Sakagami and Moure 1965; Tierney et al. 2008), and large body size is thought to be associated with social dominance (Arneson and Wcislo 2003; Smith et al. 2008). An ovarian index was measured (sum of three largest oocytes/ intertegular width) to account for the scaling effects of body size on ovary size. In multifemale nests (Table 2) only one female possessed enlarged ovarioles and in nests 12 and 13 these individuals also displayed more wing wear than their nestmates. In nests 13 (eight females) and 6 (two females) the reproductive individuals were macrocephalic (per Sakagami and Moure 1965), but in nest 12 both females were of similar body size, the slightly smaller one being the reproductive individual. These

Table 2. Reproductive status within multifemale nests of *Megalopta atra*.

Nest	Ovarian index	Intertegular width (mm)	Inseminated	Wing wear
6	2.94	3.48	+	0
	0.26	2.88	–	0
12	2.44	2.72	+	4
	0.42	2.88	+	0
13	2.61	3.76	+	7
	0.66	3.08	+	0
	0.51	3.00	–	0
	0.49	3.04	+	1
	0.47	2.96	–	0
	0.41	2.56	+	0
	0.38	3.04	+	0
	0.33	2.68	–	0
Single female (mean values $n=10$)	1.52	2.99	8+, 2–	1.5

Individuals listed in descending order of ovarian index, and the reproductive female in each nest is indicated in bold type.

nests showed no direct evidence of worker roles in non-reproductive bees and it may be that these colonies are only pre-reproductive assemblages, with some females possibly waiting to inherit the maternal nest or disperse. This interpretation is supported by the almost complete lack of wing wear in non-reproductive individuals (Table 2). A worker caste should be characterized by reduced reproductivity and evident wing wear.

Twenty-two *M. atra* (21 females, one male) were collected at light traps between 05.15 and 06.13 h at the STRI station (~1235 m) on the continental divide and at the Caribbean slope site *a* (~1160 m). Traps set at slope sites *b* and *c* (~1010 m and 664 m, respectively) attracted the two other species of nocturnal *Megalopta* commonly found in Panama (*M. genalis* and *M. ecuadoria* – see Moure and Hurd 1987; Wcislo et al. 2004), but these lower elevation traps did not attract *M. atra*, which has been collected only at higher elevations (see Engel 2006).

Discussion

Environmental conditions may lessen the probability for eusociality to occur, as the result of a shorter foraging season, constraining life cycles such that there is insufficient time for adults reared in the first brood to rear through a second brood of potential reproductives. Studies comparing populations of temperate halictine bees have shown that populations at higher altitudes (e.g., 2850 m, Eickwort et al. 1996) tend to be solitary, while populations at lower elevations are social (Sakagami and Munukata 1972; Soucy 2002). The same preclusion of sociality occurs in a halictine bee with regard to higher latitudes (Packer 1990), as expected based on biogeographic parallels between increasing altitude and increasing latitude in temperate zones (Merriam 1895). However, a subsequent phylogeographic study

utilizing mitochondrial sequence data (Soucy and Danforth 2002) proposed that solitary and social populations of North American *Halictus rubicundus* are genetically distinct lineages, and that this may be evidence for some degree of genetic determination of social behaviour.

Geographic seasonal restrictions mentioned for these halictines are for temperate taxa. A tropical social spider *Anelosimus eximius* shows an increase in the proportion of solitary webs at altitudes between 700 m and 1200 m (Purcell and Aviles 2007), although social colonies are not excluded at these upper altitudes. In other tropical halictines, social species (e.g., *Lasioglossum aeneiventre*) and species that are largely solitary (e.g., *Lasioglossum figueresi*) occur at similar altitudes >1200 m (Wcislo et al. 1993). Given that temperatures are equable year-round at midlevel altitudes in the tropics, seasonal constraints associated with temperature may be less important than phenological flowering patterns, which are lacking for the Fortuna region.

Temperature during brood rearing has also been proposed to account for the variation in body size among temperate halictines, both positively (Yanega 1989; Richards and Packer 1996; Soucy 2002) and negatively (Kamm 1974; Plateaux-Quénu 1993). Yanega (1989) and Soucy (2002) suggest that the actual length of the brood rearing season, and so greater variations in temperature, may be more important in defining this variation in size within a population. However, this reasoning cannot account for the highly variable cephalic and body sizes found among Neotropical augochlorines, where seasonal temperatures are less variable and polymorphisms are more extreme (Sakagami and Moure 1965; Tierney et al. 2008). For *Megalopta*, body size appears to be an important factor determining social reproductive status (Arneson and Wcislo 2003), although whether size differences are environmentally determined by floral availability, or by the reduction of pollen provisions by brood cell parasites (Smith et al. 2008), requires additional data and broader assessment.

Megalopta atra was not found at altitudes lower than ~1160 m and other species of *Megalopta* common to Panama were found up to ~1010 m. We are unaware of the upper altitudinal range of *M. atra*, but the species extends at least into Costa Rica (Engel 2006). Although this study does not involve an intraspecific comparison of populations at different altitudes, *M. atra* does appear to be isolated by altitude, and therefore provides a valuable comparison with lowland congeners, *M. genalis* and *M. ecuadoria* (e.g., Smith et al. 2003, 2007; Wcislo et al. 2004), and a comparative phylogeographic study of these species should be informative (*cf.* Soucy and Danforth 2002). These lowland studies detail much higher rates (percentages) of multifemale social nesting and it may be that the largest colony of *M. atra* described here is only a reflection of the larger size of the nesting substrate. It may also be presumed that the cooler mean temperatures in Fortuna would both shorten foraging times and slow the developmental time of immature *M. atra* (approximate average minimum temperatures: BCI, 22–25°C; Fortuna, 14–17°C). However, initial predawn flight times (both the coldest period of the day and the major foraging period) recorded for *M. atra* do not differ greatly from those recorded for other *Megalopta* species on BCI (~05.00–05.10 h) based on activity at nests (Wcislo et al. 2004; Kelber et al. 2006), and this suggests that *M. atra* bees do not leave the nest in the morning until astronomical twilight begins. Our data on foraging times were inferred from captures at light traps. Flight times of *M. genalis* and *M. ecuadoria* on BCI that were inferred from light-trap data (Roulston 1997) approximately

correspond to patterns of observed foraging behaviour from nests (Wcislo et al. 2004; Kelber et al. 2006), suggesting that our data provide a reasonable estimate of foraging times. Whether climate in this context effectively reduces social nesting of *M. atra* in this highland habitat remains equivocal. Longer-term studies to assess seasonal variation are required to test these assumptions.

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