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Body Size Shapes Caste Expression, and Cleptoparasitism Reduces Body Size in the Facultatively Eusocial Bees *Megalopta* (Hymenoptera: Halictidae)

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Abstract We used the facultatively social sweat bee *Megalopta genalis* (Halictidae) to test whether body size is associated with social caste. Behavioral observations showed that non-reproductive foragers were significantly smaller than reproductive nest mate queens, and foragers were also smaller than presumed pre-dispersal reproductives. Moreover, among females from field-collected nests without behavioral observations, relative body size correlated with relative ovary size. Reproductive status is not a direct result of body size, as body size was not significantly associated with either ovary size or fecundity among both solitary and social reproductives. Reproductive status is apparently an outcome of social competition for reproductive dominance, and status is influenced by size relative to nest mates. Our study is the first to demonstrate an association of body size with caste expression in a facultatively social species with relatively weak seasonal constraints on independent nesting. Larvae of a parasitic fly (*Fiebrigella* sp., Chloropidae) consume pollen provisions stored in nest cells of *M. genalis* and *M. ecuadoria*. We tested whether fly parasitism of *M. genalis* reduces body size. Parasitized females are significantly smaller as adults than their unparasitized nestmates. This reduction is of a similar magnitude to the size differences between

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castes, and has the potential to shape host reproductive options by influencing competition with nest mates. We present data on the prevalence of parasitism from four collections of *M. genalis* and two collections of *M. ecuadoria* from Barro Colorado Island, Panama, and La Selva, Costa Rica.

Keywords Body size · caste differentiation · facultative eusociality · reproductive altruism · parasitism

Introduction

Sweat bees (Halictinae) are an important taxon for investigating caste determination because of their extensive variation in social behavior among species (from solitary to obligately eusocial), and widespread within-species flexibility of social organization (Danforth and Eickwort 1997; Wcislo 1997; Richards et al. 2003; Schwarz et al. 2007). Among eusocial sweat bees, a female's caste usually depends on social competition among group mates (see Michener 1990; Wcislo 1997). Comparisons of bees from the same cohort within a nest show that replacement queens (Michener 1990; Mueller 1993) or reproductive cofoundresses (Richards and Packer 1994) tend to be larger, while foragers and guards tend to be the smaller bees. However, the importance of body size as a determinant in caste expression is complicated by the fact that temporal patterns in body size co-vary with age in species living in seasonal environments. Therefore, size and age can be confounded such that size differences may be only "an insignificant by-product" of the different times of year in which each caste is produced (Michener 1974). In fact, experimental work shows that the smallest bee can be reproductively dominant if she is also the oldest (see Michener 1990). The importance of size in within-cohort studies, though, suggests that in species that produce workers and reproductives simultaneously, size may play an important role in caste determination (Michener 1990; Mueller 1993; Richards and Packer 1994). Here we investigate the role of body size in caste determination in facultatively eusocial species (bees in the genus *Megalopta*) living in a Neotropical environment. The study population has weak seasonal constraints on reproduction. Newly emerging females may remain at their natal nest as non-reproductive workers or disperse to initiate their own nest throughout most of the year (Wcislo et al. 2004; Wcislo and Gonzalez 2006; Smith et al. 2007). If body size influences social caste, then we predict that females that express worker behavior will be small relative to their nest-mates, while reproductives will be relatively larger. Also, solitary-nesting females should be larger than workers from social nests.

Sweat bees develop inside sealed cells that are stocked with a mass of pollen and nectar, and body size is primarily determined by the amount of food in each cell (Kamm 1974; Roulston and Cane 2000, 2002). Thus, any factor that reduces the food supply can reduce adult body size, which has potential consequences for caste expression. Here we show that brood cells of the nocturnal sweat bee, *Megalopta,* are attacked by cleptoparasitic flies (*Fiebrigella* sp., Chloropidae). These flies consume some stored pollen, usually without killing the bee larva. We examined the influence of fly cleptoparasitism on bee body size. We demonstrate that fly cleptoparasitism reduces the adult body size of infected females in a dose-dependent

manner, such that cells with more fly larvae produce smaller bees. Details of these flies' life cycle, especially their activity during the tropical late wet season when *Megalopta* largely cease provisioning new cells, are unknown. The Discussion explores the role of parasites in potentially promoting worker behavior and the development of eusocial nests by handicapping parasitized females in social competition (O'Donnell 1997).

Synopsis of *Megalopta* Natural History

Megalopta females excavate nests in dry, rotting sticks that are suspended in vegetation above the ground (Wcislo et al. 2004). *M. ecuadoria* and *M. genalis* are facultatively eusocial: emerging adult females can disperse to reproduce solitarily, or remain in their natal nest and act as helpers. Nests need not have helpers: some nests remain solitary despite rearing many female offspring (Wcislo and Gonzalez 2006; Smith et al. 2007). On Barro Colorado Island (BCI), Panama, social groups typically contain two–four females and are divided into helping and reproductive castes (Wcislo et al. 2004; Smith et al. 2003, 2007). Females are presumably daughters of the foundress of the nest in which they emerge, but this has not been confirmed with genetic analyses. About one-third to one-half of all nests are multi-female during the tropical dry and early wet seasons (December–July), when the bees are most reproductively active. Nesting continues through the wet season until approximately October when provisioning largely ceases. Bees initiate new nests throughout this time (Wcislo et al. 2004). Even two-female groups express worker and reproductive castes: in each of eight observation nests studied on BCI, one bee performed more than 90% of all foraging trips and fed the non-foraging queen (Wcislo and Gonzalez 2006). The queen monopolized reproduction by actively excluding other bees from the food-provisioned brood cells before they were sealed (Wcislo and Gonzalez 2006). Occasionally nests have a secondary forager, but other females in the nest besides the queen and forager are typically reproductive females waiting approximately 1 to 2 weeks to disperse. We refer to these bees as "in-nest females". Thus, multi-female nests may contain a queen, a non-reproductive forager, and possibly one or more in-nest females. In this study, all observations refer to *M. genalis* unless indicated otherwise.

Methods

Study Sites

Observations were made on Barro Colorado Island (9°09′ N, 79°51′ W), Republic of Panama, which is a lowland tropical semi-deciduous moist forest (see Rau 1933; Leigh 1999), and at La Selva Biological Station (10°26′ N, 83°59′ W), Costa Rica, which is a lowland tropical wet forest (see McDade et al. 1994).

Observation Nests

We used behavioral observations and body size measurements of individually marked bees to test for body size relationships with behavioral caste. We modified

19 naturally occurring *M. genalis* nests for observation. To enable observation, we cut away part of the side of the nest stick to create a ~20 cm long window that was covered with transparent acetate secured with rubber bands. We then hung the nest inside an opaque polyvinyl chloride pipe. One end of the pipe was sealed, and the other end was covered with opaque plastic through which the nest entrance and approximately first 2 cm of the nest stick protruded. We checked nest contents weekly, but except for these instances the portion of the nest that we exposed for observation was protected from light and water inside the pipe, while the bees could enter and exit their nest normally through the unmodified entrance. We marked all adult female bees on the thorax with unique combinations of white dots from a waterproof paint pen.

Foraging Observations and Queen Removals

We used observations of foraging behavior to determine caste, as the queen performs fewer than 10% of all foraging trips in multi-female *Megalopta* nests (Wcislo and Gonzalez 2006). We performed all observations between late January and early March, 2004. We recorded foraging trips using a Sony MiniDV infrared camcorder mounted on a tripod at the nest entrance during the two periods of *Megalopta* foraging activity: the approximately 90 min before sunrise and 1 h after sunset (Wcislo et al. 2004; Kelber et al. 2006). After at least five observed foraging trips, we assigned bees to one of three behavioral classes: reproductive queens, primary foragers, and other "in-nest" females. We designated the female that made the most trips as the primary forager, and the other female as the queen. In-nest females, if present, were distinguished from the previous two groups by their lack of foraging, undeveloped ovaries, and their younger age. These designations were later confirmed by examining degree of ovarian development through dissections. After observing foraging behavior, we collected all adult females other than the primary forager by placing a net over the nest entrance and tapping the side of the nest to flush the bees into the net. We immediately placed the bees' abdomens into Kahle's fixative and the rest of their bodies into 100% ethanol. We collected the foragers 4 weeks after removing their nest mates, because they were part of a separate study to test for flexibility in caste expression (Smith 2005).

Dissections and Body Size Measurements

To measure ovary size, we dissected the bees' abdomens by removing the tergites and exposing the ovaries. We photographed the ovaries dorsally at ×20 magnification through a dissecting microscope with a digital camera at 2,272×1,720 pixels resolution. We calculated total ovary area from the digital photographs using Adobe Photoshop 6.0, calibrated with similarly produced digital photographs of a stage micrometer (Reichert CAT 1400). We report the mean of the left and right ovary areas as "ovary size". To obtain a population estimate of ovarian size of reproductively active females, we dissected and measured the ovaries of 21 females from solitary nests that were actively provisioning brood cells (collected on BCI, March 3–24, 2004). Because we had no a priori knowledge of the minimum ovary size necessary for reproduction, we used the smallest value from this group of

females known to be reproductively active (because they were the sole females present in nests collected with recently provisioned brood cells) as the minimum size cut-off for classifying ovaries as "reproductive."

To correlate caste with body size for *M. genalis*, we measured thorax width (taken as the distance between the tegulae) and head width (the distance across the eyes and head, measured through the antennal sockets and perpendicular to the frontal midline) from digital photographs as above, except in the case of two primary foragers that disappeared before collection, for which measurements taken with calipers at the time of their marking were used. Thorax and head width showed similar patterns in all of our analyses (see Results, below), so we used their average for each bee as an index of "body size" in further analyses. ARS did all the photography and measurements to eliminate inter-observer error.

Nest Collections

We collected additional nests from the field to survey parasite prevalence, to collect adult nest mates for analyzing body size and ovarian development, and to obtain immature bees for our rearing study. Nests were collected during the middle of the day when all adults were inside by plugging the nest entrance with cotton, wrapping the entire nest stick in a plastic bag, and bringing it into the laboratory for dissection. The La Selva nests were collected on May 23, 2003. We collected one set of nests on BCI between May 12–June 16, 2003, and another between January 19 and May 11, 2007. These two samples were used to test for the effect of fly parasitism on body size (see "rearing" below). The multi-female nests from the 2003 BCI sample (n=11) and others collected March 3–24, 2004 on BCI (n=11) were combined to analyze the relationship between ovary size and body size. We pooled the BCI data because the different samples did not differ significantly in queen mean ovary area, head width, or thorax width (Queen ovary size: mean=2.90±0.15 SE mm^2 in 2003, 3.01±0.21 mm^2 in 2004; thorax width: mean=2.94±0.25 mm in 2003, 2.93±0.16 mm in 2004; head width: mean=4.18±0.36 mm in 2003, 4.29±0.28 mm in 2004; all t-tests $p>0.05$). Females from an additional 24 nests collected between February and April, 2003 on BCI were included in the analysis of within- versus between-nest variance. The 21 single-female nests used to determine minimum ovary size for actively reproducing bees were collected on BCI March 3–24, 2004. An additional 26 nests were collected on BCI between May 6 and May 24, 2006 and surveyed for frequency of parasitism.

Bee and Parasite Rearing

We reared immature nest mate females from parasitized and unparasitized cells to test for the effects of parasitism on adult body size. We included nests from which we were able to rear at least one parasitized and at least one unparasitized female (n=8 *M. genalis*; n=3 *M. ecuadoria*). We opened the nests and moved immature *Megalopta* from their nest cells into the wells of a tissue culture plate. Immature bees were kept at ambient temperature until emergence as adults, at which point they were placed into 95% ethanol until measurement. Flies were detected and counted as either larvae living in the pollen mass of a *Megalopta* cell

or by their pupal cases left in the *Megalopta* cell. This method is likely to slightly underestimate fly parasitism because pollen masses with fly eggs that had not yet developed into larvae would not be counted (the tiny eggs are extremely difficult to detect). Also, flies occasionally pupate in the nest tunnel, presumably because the larvae finished feeding before the bee sealed the infected cell. These flies could not be assigned to any individual bee.

Statistics

All statistics were done using SPSS 10.0. We used univariate general linear models (GLM) with nest entered as a fixed effect to analyze the relationships between body size and other variables while accounting for potential non-independence of nest mates. In our analysis of size differences between castes, we used body size as the dependent variable and caste as a second fixed effect. In our analyses of fly parasitism and body size, body size was the dependent variable and presence or absence of flies in the natal cell was entered as a random effect. Because we only had three *M. ecuadoria* nests with at least one parasitized and one unparasitized female emergence, we limited this analysis to nests of *M. genalis.* We used multiple regression to analyze the effect of relative body size on relative ovary size, and number of flies in brood cells on relative body size. For both analyses, we included the variable of interest in the first step, and nest identity in the second step to account for potential non-independence of nest mates. The expected values for a Chi-square test comparing the distribution of ovary and body sizes in field-collected nests were based on the null assumption that all females in the nest are equally likely to have the largest ovaries (e.g. among three-female nests, one-third of the largest bees would also have the largest ovaries). All means are reported ±SE.

Results

Body Size and Caste Body size relative to nest mates predicts behavioral caste in *M. genalis*. In our behavioral observation nests, smaller bees were more likely to be foragers (forager mean thorax width: 2.77±0.05 mm, mean head width: 3.92±0.09 mm. Queens: 3.12±0.07, 4.39±0.11. In-nest females: 3.08±0.08, 4.35±0.14). Because head and thorax width showed similar patterns, we use their average as a measure of "body size" for all further analyses. Body size differed significantly between foragers and the other two behavioral classes of bees (GLM: behavioral class $F_{2,25}$=6.85, p=0.004; Fig. 1) but the effect of nest was not significant (nest $F_{18,25}$=0.88, p=0.61). Primary foragers were significantly smaller than both other groups (queens: n=19 nests, Tukey post-hoc comparison: p=0.004; in-nest females: n=9 nests, p=0.03), but queens and in-nest females did not differ (n=9 nests, p=0.96). Only two nests had larger foragers than queens, and these were the two smallest queens in the study.

In field-collected, multi-female *M. genalis* nests, larger bees were more likely to have larger ovaries. The largest female in a social group was most likely to have the largest ovaries (18 of 22 nests, X^2=7.47, p=0.006), and difference from nest mean body size was positively associated with difference from nest mean ovary size (n=

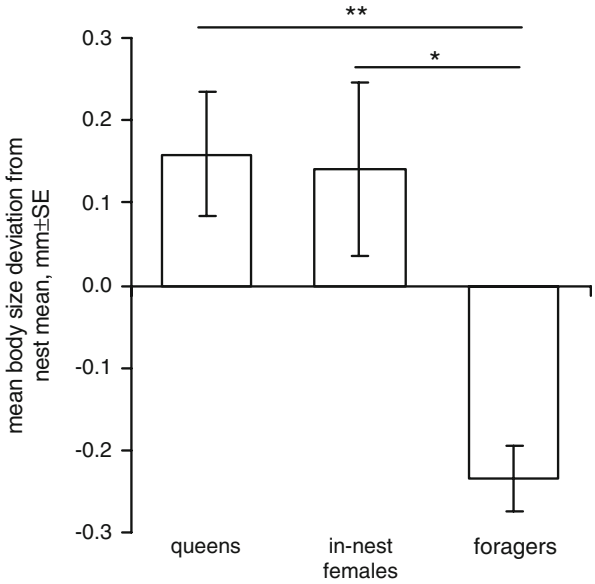

Fig. 1 *M. genalis* foragers are smaller-bodied than queens and in-nest females from their nests. The *y*-axis shows the deviation from the mean body size of the bees in the nest from which each female was collected. Each *bar* represents the mean for that behavioral caste. Significant differences in body size between castes are indicated by (*) for $p<0.05$ and (**) for $p<0.01$.

52, $r^2=0.33$, $p<0.001$, Fig. 2; including a term for nest identity did not significantly improve the fit of the model).

The relationship between body size and reproductive status is likely due to the effect of body size on behavioral caste rather than body size per se. Linear regression analysis of the 19 queens from the behavioral observation nests shows no effect of body size on ovary size ($r^2=0.007$, $p=0.74$). Likewise, among the 22 presumed queens from the field-collected nests (the presumed queen is the female with the largest ovaries in each nest), there was also no effect of body size on ovary size ($r^2=0.05$, $p=0.32$). Furthermore, there was no effect of body size on fecundity as measured by the number of brood cells upon collection ($r^2=0.04$, $p=0.42$).

Compared to the bees of known caste from our observation nests, solitarily nesting females were similar in size (thorax=3.09±0.10 mm, head=4.25±0.09, $n=21$) to queens and in-nest females, but significantly larger than primary foragers (One-way analysis of variance (ANOVA) on body size: $F_{3,63}=5.78$, $p=0.01$. Tukey post-hoc comparison vs. primary foragers $p=0.02$; comparisons vs. queens and in-nest females NS).

An ANOVA of the body sizes of the females from the behavioral observation nests, field-collected nests, and other *M. genalis* nests collected in 2003 reveals that most body size variance is within, rather than between nests (62.2% and 37.8% of type III sum of squares, respectively; $F_{66,151}=1.39$, $p=0.05$).

We do not know the minimum ovary size of a reproductively active female, so we defined "enlarged ovaries" as ≥1.56 mm^2, because this was the smallest mean ovary area value measured in 21 solitary nesting *M. genalis* females known to be

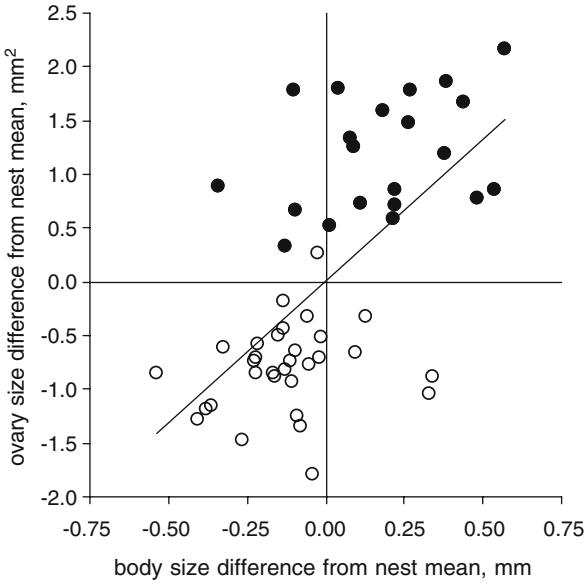

Fig. 2 Larger *M. genalis* females are more likely than their nest mates to have enlarged ovaries. Both body size and ovary size for each female are plotted as the difference from the mean value of the nest from which each female was collected. The *horizontal* and *vertical lines* represent the zero values for the *y* and *x* axes, respectively, and the *diagonal line* is a linear regression (r^2=0.33). *Closed circles* represent females with the largest ovaries in their nest (presumed queens) and *open circles* represent other females. Note that most of the bees (43/52) are either below their nest average for both body size and ovary size, or above their nest average for both.

reproductively active. In our behavioral observation nests, all of the females that we designated as queens based on observations of foraging trips had enlarged ovaries similar in size to presumed queens of field-collected multi-female nests (observation nests: n=19, ovary size mean=2.72±0.13 mm^2; field-collected nests: n=22, ovary size mean 2.88±0.15 mm^2; t=0.83, df=36, p=0.45), and all members of both groups had ovaries with a mean area >1.56 mm^2 (n=39, range=1.60–4.11 mm^2). The ovaries of the in-nest females from the behavioral observation nests were significantly smaller than the queens' ovaries (n=9 nests, mean=0.54±0.05 mm^2, GLM: behavioral class $F_{1,9}$=273.24, p<0.001; nest $F_{8,9}$=1.03, p=0.48), and all were <1.56 mm^2. We did not collect and dissect the foragers immediately because they were part of a study to test for caste flexibility (Smith 2005). However, only 9% of the field-collected multi-female nests (n=22) contained a second female with enlarged ovaries, suggesting that most foragers in the behavioral observation nests also had small, non-reproductive ovaries.

Fly Parasitism

M. genalis females reared from cells infected with flies were smaller than their unparasitized nestmates (mean parasitized body size: 3.45±0.10 mm, n=13 bees from eight nests. Mean unparasitized body size: 3.65±0.09 mm, n=14 bees. GLM: effect of parasitism: $F_{1,18}$=18.99, p<0.001; nest: $F_{7,18}$=9.59, p<0.001). Although

there was a significant effect of nest on body size, there was no nest by parasitism interaction (p=0.73). Body size relative to nestmates, expressed as the percent of mean unparasitized nest mate body size, decreased in a dose-dependent manner with the number of flies in the brood cell (n=8 nests, 27 females; r^2=0.41, p<0.001, Fig. 3; including a term for nest identity did not significantly improve the fit of the model). *M. genalis* females parasitized by flies averaged 89.19±2.3% (n=13) the body size of their unparasitized nest mates. On average foragers from the behavioral observation nests were 90.1±2.7% the size of nest mate queens, and 92.5±3.0% the size of in-nest females.

We reared parasitized and unparasitized female nestmates from only three *M. ecuadoria* nests, and all parasitized females were infected by only one fly. Each of these females was smaller than average for her nest (Fig. 3), but due to the small sample size, we did not statistically analyze these data.

Parasitism rates derived from field-collected nests varied between samples (Table 1), but overall, across both *M. genalis* and *M. ecuadoria*, 37.9% of nests had brood cells with fly parasites, and 14.3% of brood cells were parasitized. Across all samples, 65.2% of parasitized cells contained multiple flies, with a maximum of 15 flies (n=62 cells). The single dry season (January–March) *M. genalis* sample in our study (BCI 2004) showed significantly less parasitism than the three samples from the early wet season (April–June; nests: X^2=14.85, p<0.001; cells: X^2=34.15, p<0.001; Table 1).

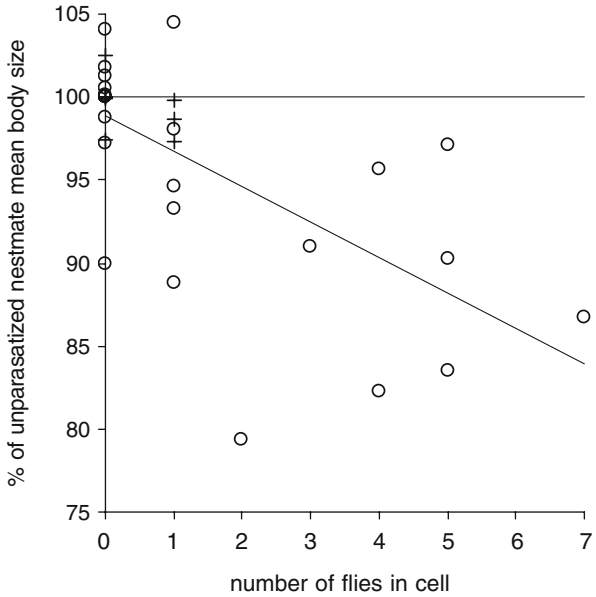

Fig. 3 Newly-emerged adult *Megalopta* females' body size relative to nest mates declines with the number of flies in their brood cell. The body size value plotted for each female is its percentage of the mean size for unparasitized nest mates. *Open circles* represent *M. genalis* females (eight nests) and *crosses* represent *M. ecuadoria* females (three nests).The *horizontal line* is the mean body size for unparasitized nest mates, and the *diagonal line* is a linear regression on the *M. genalis* data (r^2=0.41).

Table 1 Prevalence of Fly Parasitism in Four Samples of *Megalopta* Nests

Collection	Nests		Cells		Mean parasitized cells±SE per infected nest	Mean flies±SE per infected cell
	n	% parasitized	*n*	% parasitized		
BCI 2003, *M. genalis*	66	42.4	270	16.3	1.52±0.15	2.88±0.41
La Selva 2003, *M. genalis*	19	21.1	52	7.7	1±0	4.75±3.43
BCI 2004, *M. genalis*	29	6.9	154	1.3	1±0	1±0
BCI 2006, *M. genalis*	26	53.8	66	27.3	1.43±0.25	4.56±0.84
BCI 2003, *M. ecuadoria*	20	55.0	46	28.3	1.18±0.12	3.54±0.78
BCI 2006, *M. ecuadoria*	14	50.0	47	21.3	1.29±0.18	4.40±0.98

The first four collections are of *M. genalis*, and the last two are of *M. ecuadoria*

Discussion

We show that body size relative to the size of nest mates predicts both behavioral caste and reproductive status (ovary size) in *M. genalis*. Foragers tend to be smaller than both queens and in-nest females; because the in-nest females were collected, we could not determine their behavioral fates, but they were likely pre-dispersal reproductives (Wcislo and Gonzalez 2006; Smith et al. 2007). Smaller females not only tend to be foragers, but also are more likely to have undeveloped ovaries. Our analysis of the relative body size and relative ovary size of bees from field-collected nests is conservative because it likely includes young in-nest females that are large-bodied, but have not yet fully developed their ovaries, along with foragers. The relationships of body size, behavior, and ovary size that we document support previous behavioral observations of foragers being aggressively dominated by the queen and prevented from accessing brood cells (Wcislo and Gonzalez 2006). Our study is the first to demonstrate an influence of body size on caste expression in a facultatively social species with relatively weak seasonal constraints on independent nesting. Further study of other little-known tropical species may yield similar results. For instance, limited observations (N=2 nests) by Tierney et al. (2008) suggest there may be body and ovary size covariation in *Xenochlora*, which is the hypothesized sister genus to *Megalopta* (Engel 2000). Our data also support the hypothesis that small females indirectly suffer reduced fecundity because they are handicapped in social competition for reproduction, not because reproductive physiology is directly influenced by size. Among *reproductive* females, body size predicted neither ovary size nor fecundity. Thus, *Megalopta* appear to have a social system in which small differences in body size are transformed into dramatic differences in caste expression—reproductive queen or effectively sterile worker—via social competition, even when all individuals are physiologically capable of reproduction (Wcislo and Gonzalez 2006; Smith 2005; Jeanson et al. 2005).

Our data also show that fly cleptoparasitism reduces the body size of infected individuals in a dose dependent manner relative to the size of nest mates reared in uninfested cells. As discussed above, only small differences in body size are necessary to influence caste expression. *Megalopta* females are therefore susceptible to reproductive caste biasing by cleptoparasitic flies, because cleptoparasitism reduces bee body size to the same degree that characterizes observed size differences between castes. Further studies are needed to track the fates of bees reared from cells containing flies to document whether they do in fact become workers, but our data raise the possibility that fly cleptoparasitism promotes the expression of eusociality in *Megalopta* by increasing the probability that individuals remain at their natal nest as subordinate helpers.

Cleptoparasitism rates vary among nests, and nest mates vary in size in the absence of flies. Other factors, such as parental manipulation (Alexander 1974; Michener and Brothers 1974; Craig 1983; Crespi and Ragsdale 2000) or variation in resource (pollen) quantity and quality (Roulston and Cane 2002), may also generate variation in body size. The patterns that we document depend on social context: *Megalopta* caste expression is not a direct result of size per se, but of size relative to nest mates. A theoretical model predicted that parasites that physiologically castrate their hosts can promote the expression of worker behavior in those hosts (O'Donnell 1997). Our data raise the possibility that this model can be expanded to include indirect social effects, as well as direct effects on development and physiology. When there is social competition for reproduction (see West-Eberhard 1978; Michener 1990; Wcislo 1997), any parasite-induced handicap could socially castrate its host, rendering it effectively sterile. Parasites that reduce body size or otherwise lower fecundity may be more common than previously thought (Shykoff and Schmid-Hempel 1991; Hughes et al. 2003; Kudô et al. 2004; Bouwma et al. 2005). We predict that when these parasites reduce fecundity, either directly or through indirect behavioral effects, they will also promote the expression of worker behavior in their hosts (O'Donnell 1997).

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