

Dominant-subordinate Relationships in a Facultatively Social, Nocturnal Bee, *Megalopta genalis* (Hymenoptera: Halictidae)

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ABSTRACT: The potential for the formation of social relationships was explored for the facultatively social halictine bee, *Megalopta genalis*, using experimental circular arenas. Observing pairs of females from different nests, we examined the initiation of agonistic behavior, and the expression and relative frequency of dominance behavior in terms of phenotypic differences between interacting bees. Within pairs, older females with relatively larger ovaries tended to be dominant over younger females with smaller ovaries, and females with fewer nest-mates tended to initiate agonistic interactions. Bees also modified their behavior over a 24-hour time frame and were more pacific when paired with the same bee in repeated trials. Our observations suggest that these predominantly solitary bees have the capabilities to express cooperative and social dominance behavior typical of the halictines with obligate social behavior.

KEY WORDS: Halictidae; bees; dominance; agonism; social behavior.

The development and establishment of dominant-subordinate relationships within eusocial insects has been intensively investigated in groups such as paper wasps (Polistinae), honey bees (*Apis*), ants (Formicidae), and termites (Isoptera) (e.g., Hamilton, 1972; Andersson, 1984; West-Eberhard, 1987). The antecedents of such relationships have rarely been clearly identified in either smaller social groups, or in facultatively social ones, in which subordinate females may leave the nest (e.g., West-Eberhard, 1987; Vargo and Keller, 1993; Pabalan *et al.*, 2000). In some bee families, the behaviors observed in small groups may be incorporated directly into the social repertoire of larger societies (Michener *et al.*, 1971a). Analyses of such behaviors are helpful in understanding how eusociality can arise quickly from the variability inherent in less complex social arrangements (Michener, 1985; West-Eberhard, 1987; Wcislo, 1997a,b). Most studies of weakly social bees have used the behaviors of individuals as units of analysis, and in so doing confound a number of variables. As argued by Bowlby (1969) and Fogel (1995), the proper units of analyses are *relationships*, because social behavior is inherently a developmental process that unfolds within a group; therefore the phenotypes of individuals are modified by social interactions (Bateson, 1963; Kenny, 1996; Beaugrand, 1997; Wcislo, 2000).

Social organization in the subfamily Halictinae varies among and within species; many members have societies with few females, sometimes as few as two bees (Michener, 1990; Packer, 1993; Danforth and Eickwort, 1997; Yanega, 1997; Wcislo, 1997a). In most halictine groups, all females are totipotent with respect to social status when they are callow adults. Behavioral interactions among adults within nests lead to hierarchies with dominant (queens) and subordinate (worker) individuals (Buckle, 1982; Kukuk and May, 1988; reviewed in Michener, 1990). Dominance is manifested as queens frequently ram workers with their heads, prevent workers from passing by within the nest tunnels, and lead workers to the deeper regions of the nest (Michener *et al.*, 1971b; Buckle, 1985; reviewed in Michener, 1990; Wcislo, 1997a; Pabalan *et al.*, 2000).

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Studies of some temperate and tropical species report that queens tend to be larger than workers (e.g., Batra, 1966; Wille and Orozco, 1970; Kamm, 1974; Michener *et al.*, 1978; Packer, 1986; Wcislo *et al.*, 1993; reviewed in Michener, 1990; Packer, 1993; Wcislo, 1997a), thus implicating size as a causal factor in the establishment of social dominance. However, size and age can be confounded. In the laboratory, the smallest bee in a colony can be dominant if she is the oldest (Michener, 1990), suggesting that relative age also influences dominance (reviewed in Wcislo, 1997a). Age, in turn, can be confounded with residency status in a normal colony because the oldest bee is the de facto territory owner. Experimental studies of a primarily solitary sweat bee, *Lasioglossum figueresi* Wcislo (Halictidae), demonstrated that the first bee introduced into an arena more frequently became dominant, demonstrating a residency effect (Wcislo, 1997b). Similar effects have been observed among diverse territorial animals (Eshel and Sansone, 1995; Beaugrand *et al.*, 1996; Gosling *et al.*, 1996; Martinez *et al.*, 1998). Residency effects are present in other bees, such as in some solitary cavity-dwellers, where current residency usually determines the winner in contests for tunnel possession (Tepedino and Torchio, 1989; Field, 1992). Facultative cohabiting or nest-sharing bees require some behaviors that reduce levels of aggression and promote tolerance, as with other social animals (e.g., Bessékon, 1997; Moynihan, 1998). Investigations into the behavioral interactions within these flexible species may provide insight into the transitions between agonistic behavior and social tolerance.

The tropical, nocturnal bee *Megalopta genalis* Meade-Waldo (Halictidae) lives both solitarily and in small groups (2–7 bees) within the same population, making it suitable for the study of context-dependent sociality. In this study we paired *M. genalis* females from different nests to examine the connections between certain physical and environmental characteristics and the expression of dominant and submissive behavior, and to ask if behavioral differences are maintained in repeated trials. Specifically, we looked at the initiation of agonistic behavior and the relative frequency of dominance behavior expression within pairs. The following questions are addressed: (1) Do morphological characteristics such as relative body size, ovarian development, or age influence the expression of agonistic or dominance behavior? (2) Do arena “residents” (owners) tend to initiate agonism or attempt to become dominant? (3) Do solitary females tend to initiate agonistic behavior or attempt to become dominant over females with nest-mates? and (4) Are behavior frequencies consistent over 1 or 24 hour intervals?

Materials and Methods

Nest collections and behavioral observation of bees

Megalopta genalis females were collected and observed during two one-month periods, 4/20/99–5/14/99 (single trials = Series A) and 6/6/99–7/6/99 (repeated trials = Series B), during the late dry season and early wet season on Barro Colorado Island (9°N, 79°W), Panama Province, Republic of Panama. For details of the site, see Leigh (1999). Sticks with nests were collected from the field in the morning or early afternoon to ensure that all female residents were present. Nest entrances were plugged with cotton and nests were transported to the laboratory and split open with a knife. At this time of year, typically the majority of nests contained one female, and the remainder contained a small group (usually 3–5 females). Adult female nest inhabitants were captured, uniquely marked with a single dot of enamel paint, placed individually in plastic cages (volume 340–390 cm³; dimension 7 × 7 × 7 cm or 12 × 8 × 4 cm), and given 50:50 mixture of honey and water in a vial with a cotton stopper. Captured females were used in laboratory observations that

same evening. In most cases, solitary females were paired with females from multi-female nests to maximize the number of trials possible using unfamiliar bees.

We observed pairs of bees as they interacted inside a circular arena made of plastic tubing (e.g., Breed *et al.*, 1978). Clean tubing of equivalent length (30–32 cm) and inner diameter (8 mm) was used for each replicate. Trials began as the ends of the tube were joined with transparent tape to form a circle, within which bees usually walked around and encountered one another repeatedly. Observations were recorded indoors under red light illumination using a Sony TR3000 video camera with a 2+ close-up filter, between 7:30 P.M. and 12:00 A.M. Air temperatures during observations were similar to ambient temperatures (23–30°C). In other species [e.g., *Lasioglossum (Dialictus) zephyrum* (Smith)] the dominance behavior of females under these conditions is not different from the behavior observed in laboratory nests (e.g., Brothers and Michener, 1973; Bell, 1974; see Michener, 1990).

For each trial, bees were introduced to the arena in random order. One female remained in a "holding tube" (a short length of tubing) for about one minute as the other female was introduced to the arena. The bee in the holding tube was then gently prodded out and into the arena by a cotton-tipped metal probe, and the ends of the arena tubing were then joined.

In the A-series (single trials) each pair was observed for 30 minutes. In the B-series (repeated trials) each pair was observed for three 15-minute periods. The second B-series trial was conducted one hour after the first; the third trial was conducted the following evening, 22–25 hours after the second. In between B-Series trials, bees were returned to their respective cages. Females were then reintroduced to the arena in the same order as in the first trial.

The parameter "nestmate number," was used to denote a female's previous social environment, and includes the subject female (e.g., for a female with one nestmate, "nestmate number" = 2). Bees introduced first to the arena are called "residents"; all bees introduced second, from the holding tube approximately one minute later, are called "intruders."

An "encounter" between bees began when females were <7cm apart, and ended when they were ≥7cm apart. For the behaviors analyzed here, all of which took place when bees face each other, an "encounter" usually encompassed one frontal encounter (FE) as described in other studies (e.g., Kukuk, 1992; McConnel-Garner and Kukuk, 1997; Wcislo, 1997a; Paxton *et al.*, 1999; Pabalan *et al.*, 2000).

The following behaviors were analyzed:

NIP = one bee rapidly closed her mandibles <1 cm from other bee; NIPs are considered to be acts of overt aggression.

C-POSTURE = the metasoma of one bee is curled under her body, with the sting presented to the other bee; this behavior is considered an aggressive threat display, and is frequently expressed in the context of nest defense (Bell *et al.*, 1974; Bell and Hawkins, 1974).

NUDGE = one bee moved forward into close proximity (<1 cm) to the other (usually contacting the other bee's head), then moved back to her original position in a single, rapid motion. Dominant bees presumably NUDGE subordinates to attain and maintain status (Buckle, 1982; Pabalan *et al.*, 2000).

PASS = two bees move past each other in the tube without incident. Most PASSES (>99%) occurred when bees faced each other. A PASS between bees is considered an act of social tolerance.

Morphological measurements

At the end of each replicate, bees were removed from the arena, killed and dissected. Metasomata were placed in Kahle's preservative; heads with thoraces were placed in ethyl alcohol. Intertegular distance was measured for each female as an index of body size,

using a Wild M10 dissecting microscope fitted with an ocular micrometer. Mandibular wear was scored to estimate relative age (using indices from Michener and Wille, 1961); metasomata were dissected to examine both ovarian development (width of three ovarioles on the more developed side) and presence or absence of spermatozoa in the spermathecae.

Statistical analyses

Statistics were calculated using SYSTAT v7.0. Pearson correlation coefficients were used to test for relationships between morphological parameters (ovarian development, body size) and for age. Behavioral frequencies were calculated by dividing raw behavioral counts by the number of encounters observed. Non-parametric statistics were used to test for correlations between bees' behavior and phenotypic characteristics; all comparisons within the same time frame addressed separate questions and were considered independent.

Bees within each pair were designated a priori "relatively larger bee", "relatively smaller bee", "relatively older bee," etc., according to measured differences between them. Pairs with no measurable difference in a phenotype (e.g., two bees of same body size) were excluded from that phenotypic analysis (e.g., from body size analysis only). Within each analysis (e.g., body size), we used parametric T-tests to determine whether or not bees of one grouping (e.g., "relatively smaller bees," across all pairs) were significantly different (e.g., smaller) than bees of the opposing group (e.g., "relatively larger bees," across all pairs).

The expression of agonistic behaviors NIP and C-POSTURE were analyzed by recording which bee from each pair initiated the interaction. Dominance behavior (NUDGE) was not analyzed in this way, but in terms of relative frequency, because previous studies have shown that dominance hierarchies can be directly related to the frequency with which nestmates NUDGE, or ram each other with their heads (Buckle, 1982).

After scoring behaviors, we gave bees additional categorical designations according to behavioral expression, e.g., "bee to NIP first" vs. "bee that did not NIP first" or "bee that NUDGED more" vs. "bee that NUDGED less." When neither bee in a pair expressed a particular behavior, the pair was excluded from that analysis. As a result of these exclusions, a slightly different subset of pairs was used to test for correlations between each behavior and phenotype (see Table 1).

The probabilities that bees with certain phenotypes would initiate agonistic behavior or express more dominance behavior were calculated using Sign tests. Pair-level behavior (PASS frequency) was compared between time frames in Series B trials using Wilcoxon tests.

Voucher specimens

Voucher specimens are deposited in the Dry Reference Collection at the Smithsonian Tropical Research Institute (Panama), and the Natural History Museum, University of Kansas (Lawrence).

Results

Natural history of bees

In central Panama, nests of *Megalopta genalis* are found in undisturbed primary forest and secondary forest habitat (Wcislo, unpubl. data). Bees begin provisioning nests at the beginning of the dry season, late-December to mid-January, and continue through the beginning of the wet season; activity gradually diminishes throughout the wet season until the late wet season lull (roughly October through early December). *Megalopta* females

Table 1. Phenotypic measurements for pairs of bees from the same a priori designation (e.g., "larger bees") and the number of pairs used in each analysis. Means are shown with standard deviations.

"Phenotype" parameter	NIP	C-POSTURE	NUDGE
Relative body size (intertegular distance: mm)			
<i>N</i> (pairs)	21	25	28
smaller	2.86 ± 0.23	2.86 ± 0.21	2.86 ± 0.21
larger	3.11 ± 0.21	3.13 ± 0.21	3.10 ± 0.21
Relative ovary size (ovariole width: mm)			
<i>N</i> (pairs)	20	23	26
less developed	0.50 ± 0.15	0.48 ± 0.18	0.49 ± 0.71
more developed	0.80 ± 0.20	0.83 ± 0.23	0.81 ± 0.22
Relative age (mandibular wear: 1–5)			
<i>N</i> (pairs)	14	19	22
younger	1.50 ± 0.65	1.58 ± 1.02	1.48 ± 0.98
older	3.00 ± 1.00	2.79 ± 1.03	2.72 ± 0.99
Residency (lag time between resident and intruder: seconds)			
<i>N</i> (pairs)	22	26	29
	63.62 ± 22.78	65.60 ± 27.07	65.14 ± 25.69
Nest-mate number (<i>N</i> females in nest: 1–6)			
<i>N</i> (pairs)	15	19	21
fewer nest-mates	1.20 ± 0.41	1.21 ± 0.42	1.35 ± 0.89
more nest-mates	4.40 ± 0.83	4.42 ± 0.90	4.29 ± 0.90

usually construct nests in dead wood, specifically branches, vines or lianas of diameter range 1–5 cm, which are often suspended amidst a tangle of vegetation in the forest understorey. A typical nest consists of a tunnel, rarely bifurcated, running the length of the stick and containing a number of cells. A female lays an egg on a mass of nectar and pollen stored in a cell, which is then sealed. The sequence is then repeated.

Of the 62 nests used for this study, 46 (74%) contained a solitary female. Social status among cohabiting females in the 16 other nests was inferred from ovarian dissections, which suggest that social organization may vary greatly among communal, semisocial and eusocial societies (terminology follows Michener, 1974; Wcislo, 1997c). Most females used in trials were mated (>95%); 85% were reproductively active.

Social behavior

All a priori within-pair phenotypic designations (e.g., "larger bee" vs. "smaller bee" in each pair) were statistically different ($P < 0.002$ for all *t*-tests; Table 1). There was no correlation between body size and degree of ovarian development ($r = 0.16$, $N = 64$; $P > 0.05$), body size and mandibular wear (age) ($r = 0.05$, $N = 64$; $P > 0.05$), or ovarian development and mandibular wear (age) ($r = 0.02$, $N = 64$; $P > 0.05$). Therefore, these three attributes were regarded as independent for subsequent analyses.

Six (of 38) *Megalopta genalis* pairs did not interact, and were excluded from all behavioral analyses. In three out of the six non-interacting pairs, at least one female per pair had no visible wear on her wings or mandibles, and probably was recently eclosed, but all others in the non-interacting subset were worn bees. Out of 32 pairs of interacting females,

Table 2. Summary of *P* values and sample sizes for sign tests for combined A- and BI-series behavioral analyses. NIP and C-POSITION behaviors were analyzed in terms of initiation and non-initiation within pairs; NUDGE behavior was analyzed in terms of relative frequencies. Means are shown with standard deviations. Values in bold are statistically significant ($P < 0.05$).

Behavior	Body size	Ovarian development	Age	Residency status	Nestmate number
NIP initiation (<i>N</i> pairs)	0.383 (21)	0.359 (19)	1.000 (14)	0.286 (22)	0.007 (15)
C-POSITION initiation (<i>N</i> pairs)	1.000 (25)	1.000 (23)	0.359 (19)	1.000 (26)	1.000 (19)
Relative NUDGE frequency (<i>N</i> pairs)	0.850 (15)	0.011 (26)	0.004 (22)	1.000 (29)	1.000 (21)
Mean NUDGE frequency per interaction	larger: 0.315 ± 0.341	more developed: 0.975 ± 2.123	older: 0.950 ± 2.252	resident: 0.607 ± 1.936	with fewer nestmates: 0.817 ± 2.332
Mean NUDGE frequency per interaction	smaller: 0.821 ± 2.084	less developed: 0.220 ± 0.357	younger: 0.177 ± 0.247	intruder: 0.501 ± 0.829	with more nestmates: 0.451 ± 0.682

91% (29) expressed overt or 'threat' agonistic behavior (NIP or C-POSITION: at least one bee in the pair), 91% (29) expressed dominance behavior (NUDGE: at least one bee), and 69% of pairs tolerated passing.

Agonistic behavior

Using the phenotypic differences listed in Table 1, we found that the initiation of agonistic behavior (NIP or C-POSITION) in the arena was not influenced significantly by relative body size, ovarian development, or age (see Table 2).

The average lag time between the introduction of "residents" (first bees to enter the arena) and "intruders" (second bees) was 63.9 seconds ($N = 31$ pairs; minimum lag time = 25 sec; maximum lag time = 144 sec; SD = 25.6 sec) (Table 1). Residents did not tend to initiate agonistic behavior significantly more often than intruders (Table 2).

Bees with "fewer nest-mates" were usually solitary females, probably having minimal contact with conspecifics prior to capture, whereas bees with "more nest-mates" had approximately 3 nest-mates on average (see Table 1). Within pairs, the female with "fewer nest-mates" tended to initiate overt agonistic behavior (NIP) with her opponent (see Table 2). A post hoc analysis showed that these females were significantly smaller in size than their opponents and had larger ovaries (Table 3).

Dominance behavior

Relative ovary size within pairs had a significant effect on the expression of dominance behavior: females with relatively larger ovaries tended to NUDGE opponents with smaller ovaries. Age also had a significant effect: older females nudged more than their younger counterparts (Table 2).

Residents did not NUDGE more than intruders, nor did females with more nest-mates and presumably more social experience, relative to bees with "fewer nest-mates" (Table 2).

Table 3. Post-hoc analysis of the mean body size and ovarian development of females by nestmate number, and in pairs that expressed the agonistic behavior.

	N	Mean nestmate number	Mean intertegular distance (mm)	Mean ovariole width (mm)
"Fewer nestmates"	15	1.20 ± 0.41	2.89 ± 0.24	0.71 ± 0.27
"More nestmates"	15	4.40 ± 0.83	3.10 ± 0.20	0.55 ± 0.20
Paired <i>t</i> -test statistic			-2.56	1.89
d.f.			27.9	27.5
<i>P</i>			0.016	0.070

Behavioral differences over time

The repeated trials of Series B were conducted to examine the consistency of bees' behavior over time. In general, we found that the expression of behavioral differences were not consistent between initial (BI) trials and subsequent re-introductions (BII, BIII).

The majority of pairs did not express agonistic behavior in BII or BIII, whereas most did in BI (Table 4). Within four pairs that expressed C-POSITIONs in both BI and BII, the same bee consistently initiated C-POSITION in three pairs. The single bee to initiate NIP in all three trials was relatively smaller and had less-developed ovaries than her opponent.

Dominance behavior (NUDGE) was also expressed by fewer pairs in BII trials than in BI, but in contrast to agonistic behavior, increased in BIII (Table 4). The same bee NUDGED more frequently in seven out of 11 trials in which pairs expressed NUDGE in both BI and BIII.

Unlike all other behaviors, frequency of PASS increased significantly in BIII trials in comparison with BI, for pairs in which at least one PASS occurred in either trial ($N = 14$ pairs; Wilcoxon test statistic = 2.229; $P = 0.026$; see Table 4 for mean PASS frequencies for all pairs in B-trials).

Table 4. Behavioral expression between B-series trials. Mean frequencies are shown with standard deviations.

Behavior		BI trials $t = 0$	BII trials $t + 1$ hour	BIII trials $t + 24$ hours
C-POSITION	Not expressed (N pairs)	4	12	12
	Expressed (N pairs)	13	5	5
	Mean frequency per interaction ($N = 34$)	0.34 ± 0.82	0.18 ± 0.53	0.10 ± 0.31
NIP	Not expressed (N pairs)	8	13	13
	Expressed (N pairs)	9	4	4
	Mean frequency per interaction ($N = 34$)	0.13 ± 0.22	0.15 ± 0.33	0.02 ± 0.06
NUDGE	Not expressed (N pairs)	2	11	5
	Expressed (N pairs)	15	6	12
	Mean frequency per interaction ($N = 34$)	0.71 ± 1.91	0.17 ± 0.26	0.14 ± 0.24
PASS	Not expressed (N pairs)	5	11	5
	Expressed (N pairs)	12	6	12
	Mean frequency per interaction ($N = 17$)	0.29 ± 0.25	0.27 ± 0.29	0.56 ± 0.35

Discussion

Nest data from this study suggest that *Megalopta genalis* are predominantly solitary but have the behavioral capabilities necessary for cohabitation. Nearly 75% of nests (46/62) contained one solitary female; relative ovarian development between group members in many of the remaining nests was ambiguous as to which bee was the most reproductively active. The occurrence of aggressive interactions suggests that communal, egalitarian associations are rare. *Megalopta genalis* females apparently have the capacity to express behaviors associated with predominantly social bees such as *Lasioglossum zephyrum* (Michener, 1990) and *Halictus ligatus* Say (Halictidae) (Pabalan *et al.*, 2000). These observations, coupled with the fact *M. genalis* sometimes cohabit nests in nature, suggest that behaviors used in one context are co-opted for use in a variety of contexts. Defensive behavior (i.e., C-POSITION), for instance, serves as both a physical deterrent for an intruder that may get stung, as well as a visual cue for a conspecific that may interpret the behavior and act accordingly depending on the social context. Behavioral similarities between individuals across a social gradient (i.e., solitary → eusocial *sensu* Michener, 1990) imply a general flexibility which would enable short-term accommodation to local conditions. Environmental fluctuations causing sudden shortages in nesting substrate, extended flowering seasons, or increased risk of predation or parasitism, for example, can be ameliorated or exploited if behavioral elements can be co-opted for use in new or unusual contexts.

When we compared the likelihood that a bee initiated agonistic behavior in terms of a female's previous social environment, we found that females with "fewer nest-mates" (in most cases, they were solitary females) were initiators of overt aggression (NIP) more frequently than females that had "more nest-mates." Social isolation frequently results in more aggressive behavior among diverse social animals (e.g., Valzelli, 1969; Kawano, 1996). We also found that relatively older females, as well as females with relatively larger ovaries, tended to express more dominance behavior than their opponent. Thus, ovary size and age were effectively combined to produce the high frequency of dominance behavior we observed in those females. Multiple differences existed, however, within the phenotypic designations we defined. Solitary ("fewer nest-mates") females that initiated agonistic behavior, for example, also had slightly more ovarian development than opponents with "more nest-mates," and tended to be significantly smaller. Neither ovarian development nor body size alone was correlated with agonistic behavior initiation in general, but interactions between these phenotypic differences and social context may have contributed to the behavior we observed.

Contrary to a previous study using reproductively active *L. figueresi*, and work on other animals (e.g., Martinez *et al.*, 1998), "residents" did not adopt an aggressive posture, or initiate overt aggression toward opponents in the arena, more frequently than intruders. The feeble resemblance between the arena and a natural nest might contribute to this inconsistency, as well as the short lag period between the introductions of first and second bees (~1 min), although residency effects using similar arenas and lag times were demonstrated for *L. figueresi* (Wcislo, 1997b). Additionally, other aspects of life history differ between the two species that may help account for this difference. *Lasioglossum figueresi* females are active mainly in the dry season, when they produce a single generation, and individuals of two successive generations rarely overlap (Wcislo *et al.*, 1993). Consequently any adult encountered by a resident is likely to be an intra-specific parasite. In contrast, overlap of generations occurs regularly in *Megalopta*, which may be conducive to the development of tolerance through interactions with nest-mates.

Repeated trials of the same pairs of bees indicate that the outcome of prior social interactions can also influence social behavior. Passing behavior was recorded in terms of a pair-level frequency (as both bees in a pair engaged in passing more or less equally), and would be expected to remain constant over time if bees had inherent "tolerances" for unfamiliar conspecifics. The increased passing we observed over a 24-hour period (BI–BIII) may indicate that *M. genalis* females can establish social relationships and modify their behavior accordingly within such a time frame, as known for other animals (e.g., Miklósi *et al.*, 1997). Alternatively, the overnight laboratory stay of bees awaiting BIII trials may have affected their motivation to engage in social contests. Females that displayed dominance behavior (e.g., NUDGE) during the first encounter (BI) expressed the same behavior more frequently during the last encounter (BIII), suggesting that social experience as a winner enhances dominance status (see Bégin *et al.*, 1996; Ayre and Grosberg, 1995). Taken together, these data show that for *M. genalis* the behavioral components exist to facilitate the rapid expression of group-living when appropriate local conditions arise.

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