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Behavioral Interactions Among Females of *Acamptopoeum submetallicum* (Spinola) and *Nolanomelissa toroi* Rozen (Hymenoptera: Andrenidae)

Jennifer C. Grixti, Amro Zayed, and Laurence Packer

Department of Biology, York University, 4700 Keele St., Toronto, Ontario, M3J 1P3, Canada;
email: jengrixti@torontodigital.com

Abstract.—We present the results of circle tube experiments performed upon a solitary panurgine bee *Acamptopoeum submetallicum* (Spinola) and the enigmatic *Nolanomelissa toroi* Rozen. As expected for a solitary species, females of *A. submetallicum* generally avoided one another. In contrast, *N. toroi* exhibited high levels of aggression, as generally found among bees with a reproductive division of labor. However, dissection and phenological data on *N. toroi* are incompatible with either eusocial or semisocial behaviors. Furthermore, no acts of cooperation were observed in the behavioral experiments suggesting that *N. toroi* is not communal. The extremely female biased sex ratio and low levels of mandibular wear among mated, reproductively active females in this species remain difficult to explain.

Social behavior in bees varies greatly, ranging from solitary with one female per nest to eusocial with up to tens of thousands of individuals per nest (Michener 1974). A solitary bee constructs her own nest and provides stored food for her offspring, while eusocial bees (sensu Michener 1974) have a reproductive division of labor, cooperative brood rearing, and more than a single generation of adults in their nests at some point in the colony cycle. Communal behavior is a separate type of social organization in which two or more females share a nest without a reproductive division of labor. To classify the behavior of bees formally, nest excavations at various times during the nesting cycle accompanied by dissections of bees are usually needed to examine the extent of their reproductive division of labor, if any (Bell and Hawkins 1974; Brothers and Michener 1974; Wcislo et al. 1993). However, such studies are time consuming and impossible to perform in cases where nests cannot be found (Packer et al. 2003). A technique that may have the ability to quickly discriminate and classify bee social behavior without the need for detailed and laborsome nest studies, is circle tube experiments. This experimental method, introduced by Breed et al. (1978), simulates nest tunnels using clear plastic tubing, where interactions among females can be observed. Circle tube arenas were originally used to study interactions among different castes of eusocial bees (Breed et al. 1978; Pabalan et al. 2000) and to compare behaviors of species with different social organizations (Kukuk 1992; Wcislo 1997). More recently it has been used to help predict the social organization of species whose behavior is not known (Packer 2000; Packer et al. 2003).

Interactions in the circle tube apparatus are initiated when two bees encounter one another head-to-head within one body length of each other, referred to as a frontal encounter (FE). Behavioral interactions in circle tubes can usually be classified as aggressive, cooperative, or avoidance. Aggressive interactions include one or both bees nudging, lunging or biting one another. Cooperative interactions involve bees passing one another, by rotating their body in such a way that they pass venter-to-venter. Lastly, avoidance interactions involve one or both bees turning away from a FE. The relative frequency of these categories of interactions in a species seems to correspond to its social organization (McConnell-Garner and Kukuk 1997; Paxton et al. 1999; Packer et al. 2003). Intraspecific interactions among solitary bee species often result in avoidance interactions occurring at the highest frequency [e.g. *Lasioglossum figueresi* Wcislo (Wcislo 1997), *L. platycephalum* (Rayment), *L.* (*Ctenonomia*) sp. (McConnell-Garner and Kukuk 1997) and *Penapis toroi* Rozen (Packer unpublished)]. In contrast, intraspecific interactions among individuals of a communal species result in a high frequency of cooperative interactions [e.g. *Lasioglossum hemichalceum* (Cockerell) (McConnell-Garner and Kukuk 1997), *Ruizantheda mutabilis* (Spinola) (Packer unpublished) and *Panurgus calcaratus* Scopoli (Paxton et al. 1999)]. These observations intuitively agree with the behaviors expected from the above two social organizations: females in a communal nest must share the nest entrance, and thus a high level of cooperation is required, whereas solitary bees generally do not interact with other females in their nest tunnels, and thus may lack the behavioral repertoire needed for cooperation. Intraspecific interactions among individuals of eusocial bees are more complex, as different castes (queens, guards, and foragers) interact differently with each other. For example, forager-forager interactions often result in a higher frequency of cooperation, than guard—guard interactions [e.g. *Lasioglossum zephyrum* (Smith) (Breed et al. 1978)]. While queen—queen interactions often result in a high frequency of cooperative and aggressive interactions [e.g. *Halictus ligatus* Say (Pabalan et al. 2000)]. Similarly, queen-forager interactions may be cooperative, or aggressive presumably to assert dominance [e.g. *Halictus ligatus* (Pabalan et al. 2000) and *Lasioglossum zephyrum* (Breed et al. 1978)].

The behavioral repertoire of bees within the circle tube apparatus has been commonly reported for halictids (Breed et al. 1978; Smith and Weller 1989; Kukuk 1992; McConnell-Garner and Kukuk 1997; Wcislo 1997; Pabalan et al. 2000; Packer 2000; Packer et al. 2003), as they are the most behaviorally diverse bee family (reviewed by Packer 1997; Wcislo and Danforth 1997). In comparison, the behavioral repertoire of bees within the family Andrenidae, has been studied only once using these methods (Paxton et al. 1999). Although most andrenid species are solitary, some are communal (Paxton 1999; Michener 2000), while none are known to be semisocial or eusocial. Using the circle tube apparatus, social interactions between pairs of conspecific females of two communal andrenids, *Andrena scotica* Perkins and *Panurgus calcaratus* Scopoli were described by Paxton et al. (1999). *P. calcaratus* displayed highly cooperative behavior, while *A. scotica* displayed lower levels of cooperation but both displayed very low levels of aggression.

Nolanomelissa toroi Rozen, a recently described genus and species from the southern border of the Atacama Desert in Chile (Rozen 2003), has defied the attempts of several melittologists to find its nest in places where it is abundant. Furthermore, it has an extremely female biased sex ratio: only three males have been seen after extensive collecting, whereas hundreds of females have been observed. This study was conducted to examine if circle tube experiments could help establish whether *N. toroi* is a communal species, with perhaps few nest entrances per female and intranidal mating, thereby explaining the biased sex ratio. Communal behavior is well known in the subfamily Panurginae [e.g. *Macrotera texana* (Cresson) (Neff and Danforth 1992), *Perdita portalis* Timberlake (Danforth 1991), *Perdita* *opuntiae* Cockerell (Custer 1928), *Panurgus calcaratus* (Scopoli) (Knerer 1980), *Panurginus albopilosus* Lucas (Rozen 1971) and *Meliturgula braunsi* Friese (Rozen 1968)], and also in halictids [e.g. *Lasioglossum hemichalceum* (= *L. erythrurum*) (Kukuk and Schwartz 1987; Kukuk and Crozier 1990) and some species of *Agapostemon* (Janjic and Packer 2003)]. On the assumption that *N. toroi* is communal, we hypothesize that its behavior in circle tubes should be consistent with this type of social organization: interacting females should show comparatively high levels of cooperation and little aggression. *Acamptopoeum submetallicum* (Spinola), a predominantly solitary andrenid (Rozen and Yanega 1999), was also studied for comparative purposes. *Acamptopoeum submetallicum* occurs in the same subfamily as *N. toroi*, the Panurgine (Ruz 1987), with the former belonging to tribe Calliopsini Robertson, and the latter belonging to the tribe Nolanomelissini Rozen and Ascher, which appears to be the sister group to all other Panurginae (Rozen 2003, Ascher in Rozen 2003). We expect avoidance, with little cooperation, to be the common mode of interaction between *A. submetallicum* females.

METHODS

Acamptopoeum submetallicum females were collected over a nesting aggregation near Parque National Fray Jorge, Region IV, Chile (S30°38'W71°36'), on Nov. 13, 2002, from 11:00 AM to 1:30 PM. *Nolanomelissa toroi* females were collected as they visited the flowers of *Nolana rostrata* (Lindley), located approximately 9 km north of Vallenar, Region III, Chile (S28°31'W70°44'), on Nov. 17, 2002, between 11:00 AM and 1:00 PM.

Circle tube experiments were conducted on collected pairs of females of *A. submetallicum* and *N. toroi*, within 5 minutes of their capture. In an outdoor shaded area, bees were placed in 20 cm long clear plastic tubes (internal diameter 5mm) joined end-to-end to form a circle such that bees are forced to repeatedly interact with one another (Breed et al. 1978). The bees were unmarked, as marking has been shown to influence behavior (Packer submitted). The behaviors of two pairs of bees were simultaneously recorded for 15 minutes, following their introduction into the tubes. All trials were recorded using a digital camera (Sony DCR-TRV25) and interactions were scored from the resulting video. After each trial the tubes were discarded and new ones were used for the next set of trials, preventing possible pheromone contamination among pairs of bees (Smith and Weller 1989). The paired bees were then preserved in Kahle's solution for dissection. A total of 10 trials were conducted for each species. A behavioral interaction was only recorded for those interactions that followed a FE. Interactions were classified as avoidance, if one or both bees turned or backed away from a FE, cooperative if the bees passed each other or aggressive if one or both bees nudged, lunged, bit, or fought one another. Fights involved continued contact for several seconds, and in some instances, several minutes, during which a series of aggressive interactions occurred successively. Every FE ended either in a pass or avoidance interaction. In instances where a FE was followed by an aggressive interaction, and ended in a pass, both interactions were scored separately. However, if the aggressive interaction was ended by one or both bees backing away, only the aggressive interaction was scored. The proportion of the three categories of behavioral interactions was calculated as the frequency of that behavior divided by the total number of FEs during a circle tube trial.

Bees preserved in Kahle's solution were dissected using a dissection microscope (at 64 x magnification) to compare ovarian development among females, and determine whether or not they had mated. Ovarian development was established by scoring each of the six ovarioles as a fraction of a fully developed oocyte (a fully

Table 1. Frequency of occurrence of different behavioral interactions in *Acamptopoeum submetallicum* and *Nolanomelissa toroi.*

		Pair									
Species	Behavior	1	2	3	4	5	6	7	8	9	10
A. submetallicum	Aggressive	1	1	2	2	1	2	1	0.0	0.0	1
	Avoidance	5	4	12	11	13	4	12	6	0.0	3
	Cooperative	0.0	0.0	1	0.0	0.0	1	0.0	0.0	0.0	0.0
% of total	Aggressive	16.7	20.0	13.3	15.4	7.1	28.6	7.7	0.0	0.0	25.0
	Avoidance	83.3	80.0	80.0	84.6	92.9	57.1	92.3	100.0	0.0	75.0
	Cooperative	0.0	0.0	6.7	0.0	0.0	14.3	0.0	0.0	0.0	0.0
N. toroi	Aggressive	4	2	22	1	14	2	17	13	22	21
	Avoidance	4	1	15	0.0	11	6	8	9	11	8
	Cooperative	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
% of total	Aggressive	50.0	66.7	59.5	100.0	56.0	25.0	68.0	59.1	66.7	72.4
	Avoidance	50.0	33.3	40.5	0.0	44.0	75.0	32.0	40.9	33.3	27.6
	Cooperative	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

developed oocyte was scored 1), following standard methods. Each female's spermatheca was examined to determine whether they contained spermatozoa. The spermatheca of a mated female appears opaque, while in unmated females it is clear and glass-like (Packer 2000).

The head width of each female was measured as an estimator of body size (at 40 x magnification). Wing wear was measured by counting the number of nicks in the margin of one forewing, as an estimator of combined age and activity, following Ordway (1965). Bees with the entire margin abraded were given a score of 20. Mandibular wear, also an estimator of combined age and activity, was measured (at 16 x magnification) by giving a score from 0 to 10: 0 for unworn mandibles, to 10 for mandibles worn to short stumps (Ordway 1965). While it is more normal in studies of halictine bees for mandibular wear to be scored only from 0 to 5, the abrasion of mandibles close to their bases, as found here, has not been reported for these bees, hence the expanded scale.

Significant differences in circle tube behavior between *A. submetallicum* and *N. toroi* were detected using the Mann-Whitney U test with a sequential Bonferroni adjustment, used for correcting multiplicity in statistical tests (Rice 1989). Differences in mean ovarian development, mandibular wear, and wing wear between the two species were examined using the Wilcoxon test. To assess if physiological differences (ovarian development) or morphological differences (size and wear) in interacting bees affect their behavior in the circle tube trials, we correlated the absolute difference in the measured parameters between the two bees participating in a trial versus the proportion of aggressive and avoidance interactions per trial for each species, using the Spearman rank correlation test.

Finally, circle tubes are usually conducted on ground nesting bees, and it is not yet certain as to whether the social organization of non-ground nesting bees could also be predicted using this same apparatus. As *N. toroi* nests have never been found, we assume it nests in the ground similar to all known species of Andrenidae (Michener 2000).

RESULTS

Acamptopoeum submetallicum.—Frontal encounters were observed at least once in 9 of the 10 trials with *A. submetallicum.* The

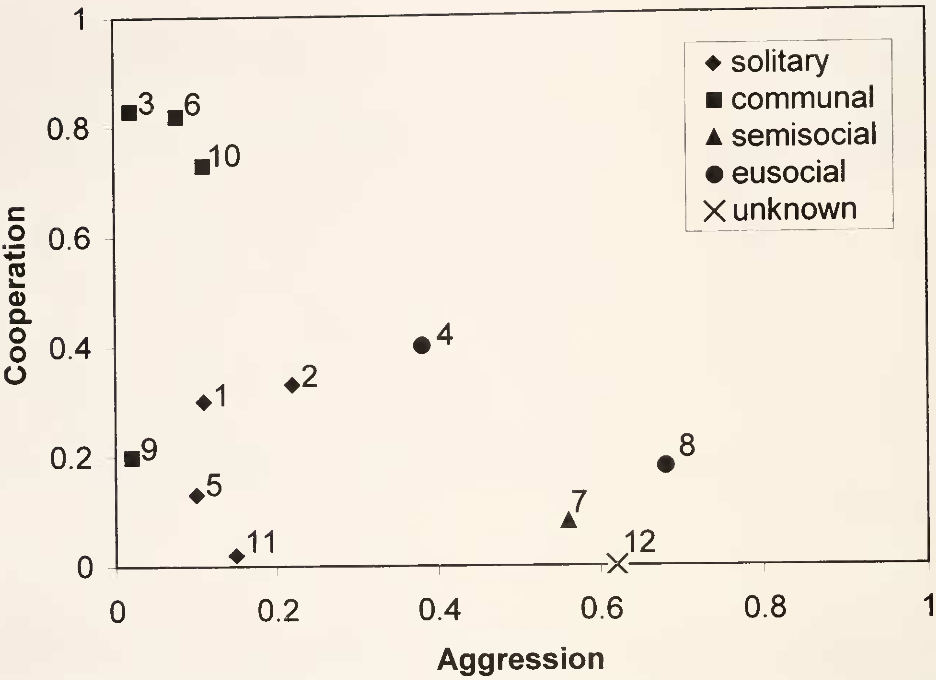

Fig. 1. Plot of the average proportion of cooperation versus aggressive interactions, grouped by social organization for the following species: 1. *Lasioglossum platycephalum*, 2. *L. (Ctenonomia) sp.*, 3. *L. hemichalceum*, 4. *L. pauxillum* (Smith and Weller 1989), 5. *Penapis toroi*, 6. *Ruizantheda mutabilis* (Spinola), 7. *Corynura chloris* (Spinola) (Packer unpublished), 8. *Halictus lanei* (Moure) (Packer et al. 2003), 9. *A. scotica*, 10. *P. calcaratus* (Paxton et al. 1999), 11. *A. submetallicum*, and 12. *N. toroi* (This study).

trial without a FE was excluded from further analysis. In total, 83 FEs were recorded in 9 trials, with an average of 9.22 FEs per trial (SD = 4.01). Females would often stay in a FE for prolonged periods of time before an interaction was observed, ranging from several seconds to well over a minute and then either lunge, bite, or back away from the opponent. The duration of FEs was quite variable, ranging from a second to over 3 minutes, in which case a series of bites and a mandibular hold, where the mandibles of both bees are clasped together in what appears to be a prolonged bite, were observed. A sum- [illegible] of the occurrence of aggressive, co- [illegible] e and avoidance interactions be- [illegible] *ubmetallicum* females is present- [illegible] 1. Most of their interactions w [illegible] (83%) (Fig. 1), usually involving only one female backing out of a frontal encounter. 15% of all behavioral interactions were aggressive, during which bites, lunges, nudges or fights were observed. Only 2% of the interactions were cooperative passes (Fig. 1).

Mean ovarian development was 2.18 (SD = 0.60, n = 16), and all females (n = 16) were mated (Table 2). 15 of the 16 females contained at least one fully developed oocyte within an ovariole, and the remaining female contained developing oocytes. The mean head width for *A. submetallicum* females was 3.37mm (SD = 0.14, n = 16). Wing wear was highly variable: 8 females with ≤ 2 nicks on the forewing margin, 6 with a score of 20 (wherein the margin of the wing was heavily eroded, and nearly half the wing was worn off) and the remaining two each with 5 nicks.

Table 2. Dissection and body measurement averages for *A. submetallicum* (n = 16), and *N. toroi* (n = 20) females. Note: OD = ovarian development, MW = mandibular wear, WW = wing wear, HW = head width and WL = wing length.

Bee species	OD	Mated	MW	WW	HW (mm)	WL (mm)
A. submetallicum	2.18 ± 0.59	all mated	3.09 ± 3.27	8.5 ± 9.32	3.37 ± 0.14	7.17 ± 0.33
N. toroi	1.22 ± 0.46	all mated	0.3 ± 0.66	0.25 ± 0.64	3.03 ± 0.17	7.16 ± 0.36

Similarly, mandible wear was also highly variable, with 9 females with a score ≤ 1, 4 with a score of 5 (wherein half the mandible was abraded), and 2 with a score of 10 (the mandible worn to a short stump). Differences in all the measured physiological/morphological parameters between interactants in a circle tube were not significantly correlated with the relative proportions of aggressive or avoidance interactions (Spearman rank correlation, $p \geq 0.129$ for all tests). Note that two bees from separate trials escaped during transferring attempts into Kahle's solution, and thus, could not be dissected and measured.

Nolanomelissa toroi.—Frontal encounters for *N. toroi* were frequent, occurring 193 times in 10 trials, with an average of 19.3 FEs per trial (SD = 13.0). FEs would quickly result in a bee either backing away from or acting aggressively towards its opponent. Most females were very active, consistently moving throughout the circle tube arena. A summary of the proportion of behavioral interactions between pairs of *N. toroi* females is presented in Table 1. All of the interactions were either aggressive (62%) or avoidance (38%) (Fig.1). Aggressive interactions included lunging, biting or fighting. In five instances, prolonged periods of fighting occurred, ranging from 1 to 3 minutes, during which a series of bites were observed.

Of the 20 females used in circle tube trials, 14 contained at least one fully developed oocyte within an ovariole, and 6 contained developing oocytes (Table 2). The mean ovarian development was 1.22 (SD = 0.46, n = 20), and all females were mated. The mean head width for *N. toroi* females was 3.03mm (SD = 0.17, n = 20). In contrast to *A. submetallicum*, wing wear measurements showed that the majority of bees were unworn, with 17 females with 0 nicks on the forewing margin, and 3 with 1–2 nicks on the forewing margin. Likewise, mandibular wear measurements revealed that 16 females had unworn mandibles, and 4 had their mandibles slightly worn. Similar to *A. submetallicum*, differences in all the measured physiological/morphological parameters in *N. toroi* females were not significantly correlated with aggression or avoidance interactions in the circle tube (Spearman rank correlation, $p \geq 0.201$, for all tests).

Interspecific comparisons.—*Nolanomelissa toroi* females interacted in the circle tube more often than *A. submetallicum*. On average, *N. toroi* females had twice the number of frontal encounters as *A. submetallicum* females ($t = -2.164$, df = 17, $p = 0.045$). The circle tube behavior of *N. toroi* was significantly more aggressive than that of *A. submetallicum* when using the Mann-Whitney U test and the sequential Bonferroni adjustment ($Z = -3.056$, df = 8, $p = 0.002$). However, the frequency of avoidance ($Z = -0.287$, df = 8, $p = 0.774$) and cooperative interactions ($Z = -1.534$, df = 8, $p = 0.125$) did not differ significantly between the two. *Acamptopoeum submetallicum* females participating in the circle tube experiments had significantly higher levels of ovarian development (Wilcoxon signed-rank test, $s = 433$, $z = 4.356$, $p < 0.0001$), mandibular wear (Wilcoxon signed-rank test, $s = 411$, $z = 3.935$,

$p < 0.0001$), and wing wear (Wilcoxon signed-rank test, $s = 403$, $z = 3.802$, $p = 0.0001$).

DISCUSSION

The interactions of *A. submetallicum* females in the circle tube arena agree with evidence of solitary nesting; more than 80% of frontal encounters were classified as avoidance, and very little aggression or cooperation was observed (Fig. 1). Also it seemed that *A. submetallicum* females avoided initiating interactions in the circle tube as supported by the comparatively low number of frontal encounters per trial (avg. 9 FEs in 15 min.). On the other hand, *N. toroi* interacted more frequently in the circle tube (avg. 19 FEs in 15 min.), with ~60% of all interactions being aggressive, and ~40% avoidance (Fig. 1). Morphological comparisons, with regard to wing and mandibular wear revealed that females of *N. toroi* were younger, or at least had been much less active in flight and nest excavation than those of *A. submetallicum*. This might suggest that bees are more aggressive early in the nesting cycle. However, no significant relationship was found between the frequency of aggressive behavior and relative age in either species [Spearman rank correlation: $p \geq 0.129$ (*A. submetallicum*) and $p \geq 0.201$ (*N. toroi*) for all tests].

Due to the difficulties associated with finding nests and the highly female biased sex ratio throughout its activity period, we had hypothesized that *N. toroi* might be a communal species. However, the majority of interactions among females of this species were aggressive, with not one instance of cooperative behavior observed. Such high levels of aggression are more suggestive of a reproductive division of labor. However, this species is active at most once a year (only in years in which there has been adequate winter rainfall) precluding a standard eusocial colony cycle with spring gynes and summer workers. As all females were mated and almost all had developed ovaries it seems unlikely that it is a semisocial species either.

The following is a list of the facts pertinent to the biology of *N. toroi*. 1) It appears to have an extremely female biased sex ratio, with approximately 100 females being found on flowers for every male encountered. 2) Its nests are unusually difficult to locate. 3) All females found on flowers are mated and have at least some ovarian development. 4) Considering that females foraging for pollen with developed oocytes are expected to have already excavated a nest, this species exhibits surprisingly little mandibular wear. 5) It exhibits high levels of aggressive behavior in the circle tube apparatus. 6) It is active only in spring in years in which there has been sufficient winter rainfall.

What can we conclude regarding the social biology of *N. toroi*? First, based on evidence from circle tube experiments, *N. toroi* does not exhibit a communal organization—this species clusters on the opposite behavioral spectrum to known communal andrenids and halictids (Fig. 1). Second, the presence of developed ovaries accompanied by a short activity period suggests that *N. toroi* does not have a complex social organization despite the high levels of aggression observed. It is worthwhile to note that *N. toroi* females exhibit a peculiar pygidial plate and modified hind basitibial plates (Rozen 2003), structures that are usually consistent in ground nesting bees (Rozen personal communication). This fact, accompanied by the extremely female biased sex ratio in combination with low mandibular wear and difficulty in finding nests are suggestive of perhaps an unusual choice of nest site and/or an unusual mating system.

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