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Behavioral Interactions Among Females of *Halictus (Seladonia) lanei* (Moure) (Hymenoptera: Halictidae)

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AND RONALDO ZUCCHI³

ABSTRACT: *Halictus (Seladonia) lanei* (Moure) has the most extreme cephalic dimorphism, and thereby presumably also caste dimorphism, among the halictine bees. Previously known only from a few sites in Brazil, additional localities for this species are documented, including the first records for it from Bolivia, and a distribution map is provided. In order to investigate the possible social organization of this species in the absence of nest excavations, circle tube experiments were performed. In these arenas pairs of putative workers of this species generally behaved very aggressively, on average more so than any of the other halictine species studied with this apparatus. One pair, however, acted very cooperatively and perhaps they were nestmates. The circle tube behaviors are consistent with the species being eusocial, a fact also supported by the strong size dimorphism and comparisons with its sister species.

KEY WORDS: Halictidae, social behavior, cephalic dimorphism

Halictus (Seladonia) lanei (Moure) is the only member of its genus found predominantly in South America (Wille and Michener, 1971; Janjic and Packer, 2001). Originally described on the basis of a macrocephalic specimen (Moure, 1940), putative workers, a male and an even more macrocephalic female were described by Janjic and Packer (2001) who suggested that the species was, like its close relative *H. hesperus* Smith, eusocial. The main objective of this paper is to present the results of some experiments aimed at investigating the possible social organization of this species. A second objective is to list the additional locality data for the specimens found at the Museu de Zoologia de São Paulo, Universidade de São Paulo, Brazil (MZSP-USP). An additional three specimens of *H. lanei* were found in the collection of the third author. These had been collected from the airstrip on the campus of Universidade Estadual do Mato Grosso, Campus de Nova Xavantina, (UNEMAT) Nova Xavantina, Mato Grosso, Brazil (4°41'S, 052°21'W). Consequently, we visited this locality during the period December 12–17th 2001 to look for this species. The bee was found moderately commonly on flowers around the edge of the airstrip, but despite several days of searching, no nest sites were discovered. Nonetheless, samples of females were obtained for dissection (data to be presented pending additional collections) and the species was certainly common enough for circle tube experiments to be performed upon females collected from flowers.

When it is not possible to find nests of a particular species of bee for which behavioral information is badly needed, some short-cut would be useful to establish its probable social organization. The circle tube apparatus has long been used to compare the behavioral repertoires and frequencies of behaviors within and among castes of halictine species (Breed *et al.*, 1978). More recently it has been used to compare behavioral repertoires among species (McConnell-Garner and Kukuk, 1997) and predict the social organization of species for which nests have not been located (Packer, 2000). Here we report the results of circle tube experiments performed on *H. lanei* females.

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Methods

Circle tube experiments were conducted upon pairs of bees collected from flowers within 15 minutes of their capture using procedures outlined by Packer (2000). All bees had been collecting pollen and/or nectar. The experiments were conducted outdoors but in the shade and behaviors were recorded continuously for up to three pairs simultaneously for 30 minutes following the introduction of the bees into the tubes. For each frontal encounter (defined as one or both of the bees moving such that they were within one body length of each other) the resulting interaction was described. The behaviors observed were classified as avoidance if one or both of the bees then turned away precluding any further interaction in that particular encounter. Alternatively, the bees behaved cooperatively, by passing one another (an interaction that requires coordination of movement to permit one bee to pass the other, venter to venter) or aggressively. Aggressive interactions seemed to occur at three levels, ranging from lunges (involving a bee head butting its opponent or lunging at it with open mandibles) through C-postures to fully fledged fights. Fights involved continued contact lasting at least several seconds, in which a number of different component behaviors occur in quick succession (involving C postures and bites or bite attempts). C postures involve one or both bees bending the abdomen under the thorax such that the sting and the mandibles are both directed towards the opponent. Each frontal encounter was scored for one behavioral outcome except when an aggressive initial response was followed by a cooperative one in which case one instance of each was scored. A video recording showing some aggressive interactions including a fight, can be found at www.yorku/bugsrus/laneivideo.html and diagrams of behavioral interactions equivalent to those observed here can be found in Bell and Hawkins (1974).

A previous study (Pabalan *et al.*, 2000) demonstrated temporal changes in the relative frequencies of various behaviors over time in the circle tube apparatus. We investigate this possibility here by comparing the relative frequencies of aggressive and cooperative behaviors between the first and the last 10 minutes for each pair of bees.

Results

Additional localities for *H. lanei*, number of males and females and dates of collection are presented in Table 1. The currently known distribution of the species is shown in Fig. 1.

The mean size of the 20 females used in the experiments was 1.82 mm (SD = 0.07, range 1.7 to 1.95 mm). Size differences between females in a pair averaged 4% and ranged from zero to less than 9%. All individuals had worn wings, ranging from one bee with one nick in the wing margin to 13 with the entire outer forewing margin abraded. Nonetheless, seven of them had no mandibular wear, including two individuals with the entire forewing margin abraded. All 20 individuals had undeveloped ovaries but two had mated.

The behavioral repertoire of *H. lanei* observed in the circle tubes was very similar to that found in many other halictine species. The main differences were the frequency of "fights," which are rare or absent altogether in other species, and the nature of many of the C-postures. Although the C posture adopted by females of *H. lanei* appeared identical in form to those observed in other species, it is the only species we have observed in which the bees would adopt the posture at a considerable distance from their opponent. Sometimes both individuals adopted the C posture while still several centimeters from each other and then approached one another in this posture. Such apparently high motivation for adopting an aggressive stance has not been observed in any of the other more than 20 species of halictid that the senior author has studied using the circle tube apparatus.

There was wide inter-pair variation in the relative frequency of different categories of

Table 1. List of localities and number of specimens known for *Halictus lanei*.

Locality	Date	Number of	
		Males	Females
Brazil, Rondonia, Porto Velho	iv.& xi.1964		53
Brazil, Mato Grosso, Rondonopolis	ix–xii.1964	3	5
Brazil, Mato Grosso, Nova Xavantina	xii, 2001	7	107
Brazil, Mato Grosso, Nova Xavantina	vi, 1997		1
Brazil, Mato Grosso, Nova Xavantina	vi, 1999		2
Brazil, Mato Grosso, Xingu	xi. 1964		1
Brazil, Mato Grosso, Caceres	unknown		1
Brazil, Bahia, Barra Bahia	xii. 1907		9
Brazil, Bahia, Boqueirao	i. 1908	1	
Brazil, Para, Conceição do Araguaia	vii.		1
Brazil, Goiás	unknown		1*
Bolivia, San Antonio, Parmoeti	vii.		2
Venezuela, Lara	vii		1
Venezuela, Merida	unknown		1

* This is the type specimen.

An additional two specimens have been found in the Museu de Zoologia (MZSP-USP), São Paulo from Cesar de Souza, São Paulo State. They have slightly longer heads than the other females listed above and also appear slightly darker. It is possible that they belong to a related, undescribed species.



Fig. 1. Distribution map for *Halictus lanei*. Although the two specimens from Venezuela are at some distance from the other localities for *H. lanei*, they both have the characteristics of the species as described by Janjic and Packer (2001).

Table 2. Frequency of occurrence of different behavioral categories in *Halictus lanei*.

Time period	Behaviour	Pair									
		1	2	3	4	5	6	7	8	9	10
1-10	Aggressive	16	9	9	15	10	17	2	7	23	6
	Avoidance	0	1	1	1	3	3	1	5	3	3
	Cooperative	0	0	0	0	0	22	0	0	0	0
11-20	Aggressive	12	8	7	5	3	0	6	14	25	9
	Avoidance	0	2	3	4	0	1	1	3	2	1
	Cooperative	2	1	2	0	0	58	0	0	4	0
21-30	Aggressive	12	8	7	12	2	1	9	11	18	7
	Avoidance	0	1	1	1	0	0	8	0	4	6
	Cooperative	3	0	4	1	0	79	16	2	12	0
% of total	Aggressive	88.9	83.3	67.6	86.5	83.3	9.9	39.5	76.2	72.5	68.7
	Avoidance	0.0	13.7	14.8	10.7	16.7	2.3	23.3	19.1	9.9	31.3
	Cooperative	11.1	3.3	17.6	2.7	0.0	87.8	37.2	4.7	17.6	0.0

behavior (Table 2, Fig. 2). Although most pairs were highly aggressive, one pair was highly cooperative and another exhibited intermediate levels of aggressive and cooperative behaviors. It was noticed that the most cooperative pair also had by far the largest number of frontal encounters (181 in comparison to a mean of less than 42 for the remaining nine pairs). A Spearman's coefficient of rank correlation between the proportion of frontal encounters that were cooperative and the number of interactions in 30 minutes was significant ($r_s = 0.75$, $P < 0.02$). This could suggest that bees that interacted more frequently became habituated to one another more readily and thus behaved more cooperatively. However, close inspection of the data indicates that this was probably not the case. The outlying cooperative pair was the only one to exhibit any cooperative behaviors within the first 10 minutes of interaction and indeed, their second and fourth interactions were cooperative: this pair was more cooperative than other pairs right from the beginning. The second most cooperative pair was less active ranking 6th in the number of frontal encounters over the duration of observations. In seven of the 10 pairs, the frequency of cooperative behaviors was higher in the last 10 minutes of the observations than in the first 10 minutes; a non-significant (sign test) increase in cooperation during the period of observation. Two pairs became more aggressive during the same time interval.

Discussion

Halictus lanei has the highest level of caste dimorphism of any halictine species known. Indeed, the photograph of a putative queen and worker published by Janjic and Packer (2001) is more suggestive of the extreme caste dimorphism found in many ants than it is of a sweat bee in which morphological caste differences are usually slight. This suggests that this species would be well worthy of investigation in the field. Hitherto, this would have seemed to be a daunting task as the species was known from less than 20 individuals. Now it would appear that the species is locally common, at least in some parts of Brazil (Table 1) and it is certainly common enough at the UNEMAT campus to suggest that finding nests should be possible. Nonetheless, four days of active searching by three melittologists failed to locate any nests.

Only one macrocephalic female was found during our field work (head width = 2.4 mm, with developed ovaries and inseminated; this female was not used in circle tube experiments). If this was a comparatively late foundress, this might suggest that most nests

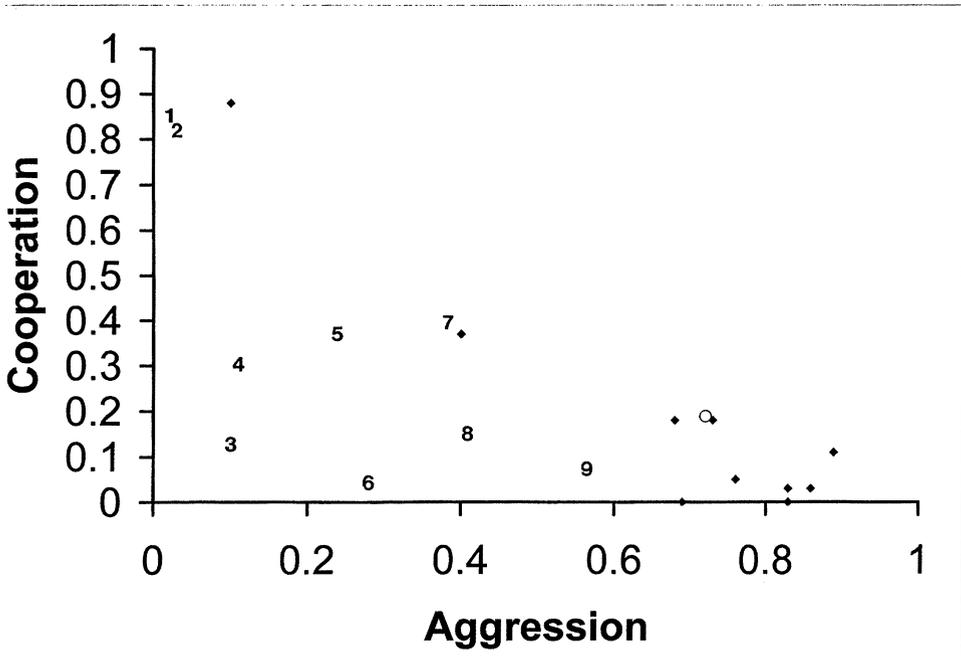


Fig. 2. Plot of levels of aggression against levels of cooperation for 10 pairs of *H. lanei* along with its average (each pair counted as equal) and with averages for other species from the literature. See text for explanation of how the levels were calculated. The other species are denoted by numbers, each pair of *H. lanei* by diamonds, the mean for *H. lanei* is shown by the circle. Other species, their sociality and reference are as follows: 1. *Lasioglossum (Chilalictus) hemichalceum* (Cockerell), communal (McConnell-Garner and Kukuk, 1997), 2. *Ruizantheda mutabilis* (Spinoza), communal, (Packer, unpublished observations), 3. *Penapis* sp. solitary (Packer, unpubl. obs.), 4. *L. (Ch.) platycephalum* (Rayment), solitary (McConnell-Garner and Kukuk, 1997), 5. *L. (Ctenonomia)* sp., solitary, (McConnell-Garner and Kukuk, 1997), 6. *Thrincohalictus prognathus* (Pérez), solitary?, (Packer, 2000), 7. *L. (Evyllaesus) pauxillum* (Schenek) eusocial, (Smith and Weller, 1989), 8. *L. (Dialictus) figueresi* Wcislo, solitary (Wcislo, 1997), 9. *Corynura chloris* (Spinoza), semisocial (Packer, unpublished observations). For the communal, eusocial and semisocial species, data presented are from pairs of females from different nests only.

had not been recently initiated and the smaller females may have been workers from the first worker brood. This would indicate that most nests were initiated in October or early November, coinciding with the beginning of the wet season in this part of Brazil. This assumes that nests are initiated more or less synchronously in this species which is certainly normally the case for halictines, albeit not without exception (Packer and Knerer, 1986). The high proportion of worker females with entirely abraded wing margins suggests that most of the bees that were active in mid December had been active for quite some time.

The extreme cephalic dimorphism among females of *H. lanei* is remarkable and suggestive of very strong caste dimorphism in a eusocial species. Although corroboration of this requires the discovery of nests, the fact that its closest relative, *H. hesperus*, is eusocial with a large caste size dimorphism along with moderately marked cephalic dimorphism (Brooks and Roubik, 1983; Packer, 1985), is supportive of this contention. Additional indirect evidence for this also comes from the circle tube experiments.

It has been argued that halictid species with a reproductive division of labor behave more aggressively in circle tube arenas than do females of solitary or communal species

(McConnell-Garner and Kukuk, 1997; Packer, 2000). Figure 2 shows the relative position of *H. lanei* with respect to the other halictine species for which circle tube data have been published and, for most of them, their social organization is known from nest excavations. Although the original published data are not always directly comparable to those collected here, the studies included did use methods similar to those described here. The data clearly show that *H. lanei* is, on average, the most aggressive species. Nonetheless, the outlying pair that was predominantly cooperative deserves some comment. These two bees did not differ in relative ovarian development or mating status in comparison to any of the other pairs and, as noted above, their high level of cooperation did not result from higher overall activity levels. They may have been nestmates and thus would have been used to interacting within the nest. This too can be tested when nests of the species are discovered.

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