Behavioral Repertoires and Interactions between Apis mellifera (Hymenoptera: Apidae) and the Native Bee Lithurgus littoralis (Hymenoptera: Megachilidae) in Flowers of Opuntia huajuapensis (Cactaceae) in the Tehuacán Desert

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Behavioral repertoires and interactions between *Apis mellifera* (Hymenoptera: Apidae) and the native bee *Lithurgus littoralis* (Hymenoptera: Megachilidae) in flowers of *Opuntia huajuapensis* (Cactaceae) in the Tehuacán desert

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Abstract

The introduction of the honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), into the arid environments of Mexico has affected the behavioral ecology of native bees. We described the behavioral repertoire and interactions between *A. mellifera* and the native bee *Lithurgus littoralis* Cockerell (Hymenoptera: Megachilidae) on *Opuntia huajuapensis* Bravo (Cactaceae) flowers in a semiarid environment. We filmed the bees in 150 cactus flowers to obtain the diversity of behaviors and their durations and thereby quantify the interactions. The behavior accumulation curve (Clench model) showed differences in the behavioral repertoire between the 2 bee species and between the sexes of *L. littoralis*. We found that *A. mellifera* and *L. littoralis* females invested more time in feeding behavior than *L. littoralis* males and recorded a wider repertoire of agonistic behaviors in male compared with female bees. Native male bees often perched in flowers and were inactive for long periods. The results indicate a possible interference competition between native and non-native bee species that are visiting the flowers of *O. huajuapensis*.

Key Words: honey bee; native bee; agonistic behavior; competition

Resumen

La introducción de la abeja europea *Apis mellifera* L. (Hymenoptera: Apidae) en los ambientes áridos de México ha afectado la ecología del comportamiento de las abejas nativas. Describimos el repertorio conductual y las interacciones entre *A. mellifera* y la abeja nativa *Lithurgus littoralis* Cockerell (Hymenoptera: Megachilidae) en flores de *Opuntia huajuapensis* Bravo (Cactaceae) en un ambiente semiárido. Filmamos las abejas en 150 flores para obtener la diversidad y duración de las conductas y cuantificamos las interacciones entre abejas exóticas y nativas. La curva de acumulación de conductas (modelo de Clench) indica que hay diferencias en el repertorio conductual de las dos especies de abejas y entre sexos de la abeja nativa. Encontramos que *A. mellifera* y las hembras de *L. littoralis* invierten más tiempo alimentándose que los machos de *L. littoralis*, y que éstos cuentan con un amplio repertorio de conductas antagónicas que contrasta con el de las hembras y que incluye permanecer inactivos en las flores por amplios lapsos de tiempo. Los resultados indican una posible interacción de competencia por interferencia entre las especies de abejas nativas y no nativas que visitan las flores de *O. huajuapensis*.

Palabras Clave: abeja europea; abejas nativas; comportamiento agonístico; competencia

The directed or unintentional introduction of non-native bees in different environments has affected native pollinators mainly because they compete for floral resources (Goulson 2003; Paini 2004). The honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), has been considered beneficial because of its importance as a generalist pollinator of many economically important plants and has, therefore, been introduced in many ecosystems. However, its introduction has had negative consequences for native biota, as *A. mellifera* can reduce the diversity of native bees due to increased competition for floral resources (Huryn 1997; Badano & Vergara 2011), and influence plant–pollinator networks (Campos-Navarrete et al. 2013). As a consequence, the introduction of non-native bee species has modified the behavior of both native and non-native bees (Goulson 2003; Thomson 2004).

The consequences are worse when non-native and native bees converge on the same floral resource, which affects their behavioral responses. Honey bees affect native solitary bees at the peak of the

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blooming season (Thomson 2016). However, Shavit et al. (2009) indicated that evidence supporting a negative effect is circumstantial and can be more severe during the dry season or during droughts when floral resources are limited. Identifying and measuring the duration and frequency of non-native and native bee behaviors and their intra and interspecific interactions allows us to understand the likely ecological and evolutionary consequences of the introduction of non-native bees (Ishii et al. 2008). This is a particularly critical subject because research suggests that successful pollination is enhanced by increased diversity of native pollinators (Peso & Richards 2010; Brittain et al. 2013).

In addition, the time spent by bees collecting floral resources and the behavioral repertoire of defense and agonistic interactions likely has important consequences on the fitness of both native and non-native pollinators. There are records of intraspecific differences in the behavioral repertoires of introduced bee species such as *A. mellifera* (Wilms & Wiechers 1997; Schlumpberger & Badano 2005) and *Bombus terrestris* L. (Hymenoptera: Apidae) (Spaethe & Weidenmüller 2002), as well as those from families of native bees including Halictidae, Megachilidae, Colletidae (Batra 1978), Anthophoridae (Stone 1995), and the family Apidae, tribe Euglossini (Dressler 1982).

Although studies of agonistic interactions between non-native and native bees have been done in tropical environments (Jha & Vandermeer 2009; Downing & Liu 2012), few studies deal with the spatial convergence of native and non-native bees in floral resources in arid and semiarid areas, where bee diversity is relatively high (Minckley et al. 2000; Golubov et al. 2010). The genus *Opuntia* has diversified extensively in Mexico in arid and semi-arid habitats. Bees from several native bee genera including *Lithurgus*, *Diadasia*, *Melissodes*, *Bombus*, *Agapostemon,* and *Megachile* visit *Opuntia* flowers (Osborn et al. 1988; McFarland et al. 1989; Mandujano et al. 1996; McIntosh 2005; Reyes-Agüero et al. 2006; Mandujano et al. 2013).

The interaction between native bees and *A. mellifera* has been studied mainly in agricultural areas (Pinkus-Rendon et al. 2005; Peters & Carroll 2012) and it is unknown if *A. mellifera*, introduced in the central region of Mexico in approximately 1760 (Labougle & Zozaya 1986), affects the behavior of native bees when interacting over flowers in other habitats. To understand the patterns of competitive interactions in arid environments, we observed native and non-native bees in the Tehuacán desert in México to determine whether individuals of the oligolectic bee *Lithurgus littoralis* Cockerell (Hymenoptera: Megachilidae) displayed agonistic behavior to *A. mellifera* and to conspecifics in flowers of *Opuntia huajuapensis* Bravo (Cactaceae).

We hypothesized that the convergence of *A. mellifera* and native bees at the same time and on the same flower would lead to an increase in the frequency and duration of agonistic behavioral displays. This would likely affect the behavior of native and *A. mellifera* bees during each conspecific or heterospecific encounter. Thus, our aim was to record the behavioral responses of *L. littoralis* and *A. mellifera* bees and their interactions in flowers of the cactus *O. huajuapensis* to address the following research objectives: (1) to describe the behavioral repertoires, (2) to compare them between species, and (3) to compare them in native male and female bees when they converge on *O. huajuapensis* flowers.

Materials and Methods

STUDY SITE

The study was conducted in the northern extreme of the Tehuacán desert, in the north central portion of the states of Veracruz and Puebla, in the locality known as "Frijol Colorado" (09.6078944°, −97.3821500°). This area is within the arid Cuenca Oriental Basin in the Mexican Trans-volcanic belt (INEGI 1998) at an altitude of 2,300 m, an average annual rainfall of 500 mm, and a mean annual temperature of 12 °C to 18 °C. The climate type is 1 of the wetter types in semiarid zones in Mexico (García 1988). A lava flow outcrop characterizes the geology of this site dominated by the arborescent monocotyledons *Nolina parviflora* (Kunth) Hemsl. (Asparagaceae) and *Yucca periculosa* Baker (Asparagaceae) (Dávila et al. 2002).

Temperature (°C), relative humidity (%), and wind speed (m per s) were measured at the beginning and end of each filming period at the floral level with a portable digital weather tracker (Kestrel 4000; Nielsen-Kellerman, McKellar, ACT, Australia). The micro-environmental conditions of flowers during the study were similar among recording times. The mean temperature was 24 ± 2.3 °C (± 1SE; coefficient of variation [CV] = 9.6%). The minimum and maximum temperatures were 13 and 28 °C, respectively, and the humidity was 35 ± 7.6% (min. 16%, max. 53%; CV = 3%) and wind speed was 2 ± 1.1 m per s (± 1SE; min. 0 m per s, max. 17 m per s; CV = 56%).

STUDY SPECIES

The cactus *Opuntia huajuapensis* occurs in the states of Puebla, Veracruz, and Oaxaca in Mexico. It has 5 to 6 cm-long yellow flowers with greenish yellow segments in the perianth (Bravo-Hollis 1978). This species blooms from May through Jun, when their flowers represent the only resource available for various pollinators, and with the native bee *L. littoralis* and the non-native *A. mellifera* as the most conspicuous species. The mean flower area in the study site was 15 ± 6.5 cm^2 at a height of 52 ± 17.6 cm (SE). The average time that flowers remained open was 1.4 ± 0.64 d as recorded in 60 flowers within the study site.

In the study area, feral colonies of *A. mellifera* visit the flowers of *O. huajuapensis,* and the native oligolectic bee *L. littoralis* was observed only during the flowering season of *O. huajuapensis*. *Lithurgus littoralis* can be recognized by its dark color and sexual dimorphism with females larger than males (13–16 and 10–13 mm, respectively).

Lithurgus littoralis was identified by Hugo Eduardo Fierros López, Centro Universitario de Ciencias Biológicas y Agropecuarias (CUCBA), Departamento de Botánica y Zoología, Universidad de Guadalajara, Zapopan, Jalisco, México and voucher specimens were deposited in the Colección Entomológica of José Luis Navarrete-Heredia.

BEHAVIORAL REPERTOIRE

Consecutively, for 5 d, at the beginning of the *O. huajuapensis* flowering season in late May 2009, we filmed 150 flowers from different plants with 2 camcorders (Sony Handycam® Camcorder, model number: DCR-DVD610; Sony Corporation, Tokyo, Japan) using a 10× zoom. The cameras were placed 1 m away from the target flowers to avoid interfering with bee behavior. The videos were recorded between 11 AM and 12 PM. Recording sessions lasted 3 min and were finished each d after each operator recorded 75 flowers. Bees were present in all cases and selected flowers had full open petals and stigma, anthers with pollen, and lacked evidences of florivory. The weather conditions in all cases were favorable for insect activity.

Each video file was analyzed frame by frame with an InterVideo WinDVR Recorder 4.5 program to annotate the behavioral repertoire of the bees (Campos-Jiménez et al. 2014). For statistical analyses, behavioral patterns were classified into 10 categories: (1) "floral visit" indicates contact of the legs with some structure of the flower; (2) "feeding" indicates collection of nectar or pollen; (3) "exploratory flights", which include sustained, fast zigzag, horizontal, S-form, U-form and near the flower flights without making contact with the flower; 4) "bee walk" on either stamens or petals of the flower; 5) "body cleaning" either head or abdomen; 6) "agonistic behavior" including fighting, biting, body contact, lunge or approach between bees in or close to the filmed flower; 7) "no activity" implying bee immobility while it was posing in the flower; (8) "rapid movement of abdomen" is self-explanatory; (9) "proboscis extension" while in the flower without doing another behavior in the flower; and (10) "leaving the flower" was moving away from the flower for at least 1 s. We also recorded the species and number of bees that performed the different behaviors, and the duration of each behavior.

INTERACTIONS BETWEEN SPECIES

The intra and interspecific interactions among bees were recorded from the videos as the number of events in which 2 species of bees visited a flower at the same time and the frequency of intra and interspecific agonistic behaviors. We also recorded the amount of time bees stayed on the flower after receiving aggression from either intra or interspecific individuals independently of the exhibited behaviors after aggression. The numbers of bees recorded per behavioral group were independent during counting because only the first behavioral event was registered.

STATISTICAL ANALYSES

The behavioral repertoire was analyzed using a Clench model, which is a mathematical function that describes the accumulation curves (Dias et al. 2009). We fitted a nested ANOVA using general linear models (GLM) to relate the number of bees, time spent per visit, and feeding duration as dependent variables (y) to bee species (a 3-level factor accounting for *A. mellifera* females and *L. littoralis* males and females) and flower identity. The model was y = bee species + bee species [filmed flower] + error, with bee species nested within the filmed flower. We considered each filmed flower as an independent observation. The dependent variables (x_i) were square root transformed to meet the assumptions of normality and homogeneity of variances (Zar 1996). Comparisons among means were done using Tukey honest significant difference tests ($P < 0.05$). To evaluate the time spent by bees in flowers, the following Pearson correlations were carried out: (1) time spent in flowers by female vs. male bees and by native species vs. *A. mellifera* and (2) feeding duration of female of *A. mellifera* vs. the duration of agonistic behavior by male bees. The agonistic interaction between bee species was compared using percentages. All analyses were performed in JMP 6.0 (SAS 2005).

Results

BEHAVIORAL REPERTOIRE

We registered 25 patterns of behavior and grouped them for analysis (Table 1). There were 15 patterns of behavior in the *A. mellifera* repertoire (Clench model: a = 0.63; b = 0.04; asymptote: 12.5; r^2 = 0.95; Fig. 1A). The repertoire of *L. littoralis* regardless of sex included 25 behaviors (Clench model: a = 4.69; b = 0.22; asymptote: 22.5; r^2 = 0.96; Fig. 1B). There were 16 behaviors in the female *L. littoralis* repertoire (Clench model: a = 0.57; b = 0.05; asymptote: 13; r^2 = 0.86; Fig. 1C). Finally, there were 23 behaviors in the repertoire of *L. littoralis* males (Clench model: a = 4.67; b = 0.25; asymptote: 21; r^2 = 0.97; Fig. 1D).

Table 1. Behavioral repertoire of *Apis mellifera* (A) and of males (L♂) and females (L♀) of *Lithurgus littoralis* exhibited on flowers of *Opuntia huajuapensis*. The 1st column indicates the 10 behavioral groups into which the 25 behavioral patterns were merged.

Behavioral group	Behavior	Bees showing the behavior
Floral visit	Flower contact	A, L♂, L♀
Feeding	Pollen collection	A, L♀
	Nectar collection	A, L♂, L♀
Exploratory flights	Sustained flight	A, L♂, L♀
	Fast zigzag	A, L♂, L♀
	Horizontal	A, L♂, L♀
	Flight in S form	A, L♂
	Flight in U form	L♂
	Near the flower without contact	A, L♂
Walks on the flower	Stamens	A, L♂, L♀
	Petals	A, L♂
Body cleaning	Head	A, L♂, L♀
	Abdomen	A, L♂, L♀
Agonistic behavior	Biting the body in flight	L♂
	Fighting in flight near the flower	L♂, L♀
	Contact fighting inside the flower	L♂, L♀
	Contact with legs in flight	L♂
	Rapid zigzag flight with body contact	L♂
	Approach without physical contact	A, L♂, L♀
	Lunge	L♂
No activity	Total immobility	L♂, L♀
	Leaving the flower	A, L♂, L♀
Movement of abdomen	Rapid movement of abdomen	L♂, L♀
Proboscis extension	Proboscis extension	A, L♂, L♀
Leaves the flower	Moving away from the flower	A, L♂, L♀

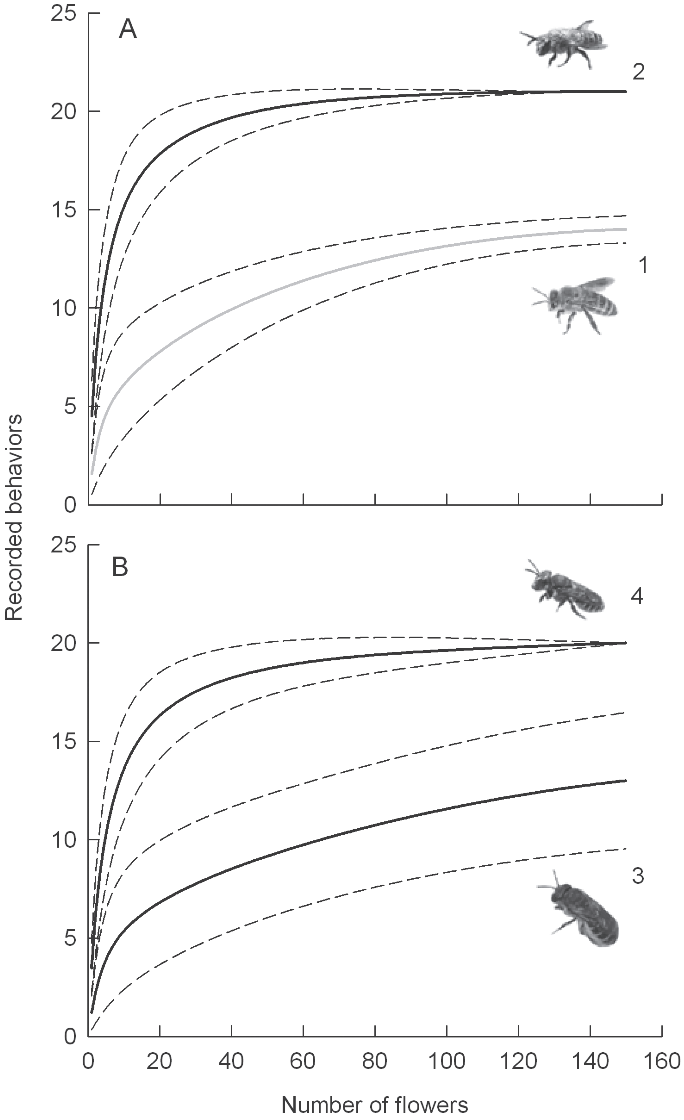

Fig. 1. Behavior accumulation curves of bees in 150 flowers of *Opuntia huajuapensis*. A: *Apis mellifera* (1) and *Lithurgus littoralis* (2). B: *L. littoralis* females (3) and *L. littoralis* males (4). Dotted lines indicate the 95% confidence intervals.

The number of bees for each behavioral group varied between species and sex. Female bees of *L. littoralis* visited more flowers but *A. mellifera* bees displayed a higher percentage of feeding behavior compared with female native bees. The exploratory flight was the most common behavior of male bees coupled with walking in the flowers and body cleaning. Nearly 14.6% of male native bees displayed agonistic behaviors in contrast to less than 1% of female native and non-native bees (Table 2). When the bees were feeding, they tilted their heads toward the base of stamens to collect nectar or assumed horizontal postures to collect pollen or to rest. A diagonally tilted position with the head pointing away from stamens and nectaries seemed to be a defensive posture from which, according to our field observations, bees were more prone to initiate attacks.

NUMBER OF BEES ON FLOWERS

On the 150 flowers, 684 bees were recorded and the number of bees varied by species and sex (*A. mellifera*: n = 123; *L. littoralis* males: n = 495; *L. littoralis* females: n = 66). The 1-way nested ANOVA indicated that there were significant differences among groups (species and sex). The means comparison tests ($P < 0.05$) indicated that the mean number of *L. littoralis* males per flower (3.2 ± 0.2) was significantly higher than that of *A. mellifera* (0.8 ± 0.09) and *L. littoralis* females (0.4 ± 0.05) and that there were no significant differences between *L. littoralis* females and *A. mellifera* (F = 3.2; df = 2, 149; r^2 = 0.81, $P <$ 0.001). A few *Diadasia* sp. (Hymenoptera: Apidae) were observed but the numbers were not sufficient for statistical analyses and no *A. mellifera* males were recorded at any time during the experiment.

DURATION OF BEHAVIORS

Apis mellifera spent more time feeding than *L. littoralis,* with the females of *L. littoralis* feeding only half the time spent by *A. mellifera*. *Lithurgus littoralis* males were inactive on the flowers a greater percentage of time compared with females (Table 3). Furthermore, male bees invested less time in direct resource defense spending only 1.53% of their total time on agonistic behavior (Table 3).

The time spent in flowers by *A. mellifera* was significantly higher than that recorded for native females and males (F = 3.8; df = 2, 149; r^2 = 0.79; P = 0.01; Fig. 2A). In this regard, there were no differences between sexes in *L. littoralis* ($P > 0.05$; Fig. 2A). The duration of feeding behavior was significantly different between species and sexes (F = 17; df = 2, 149; P <0.001). Means comparison tests ($P < 0.05$) indicated that the feeding duration was statistically similar between *A. mellifera* and *L. littoralis* females, but significantly higher when compared with *L. littoralis* males (Fig. 2B).

CORRELATION OF BEHAVIORS

There was no correlation between the time spent by female and male native bees and the time spent by *A. mellifera* (N = 138, r = 0.03, $P > 0.05$). There also was no correlation between the time spent by male and female *L. littoralis* (N = 138; r = 0.04, $P > 0.05$). Finally, the time that *L. littoralis* females fed on the flower was not significantly correlated with the time used by *L. littoralis* males for agonistic behavior (N = 138; r = 0.06, $P > 0.05$).

INTERACTIONS BETWEEN SPECIES

In 78 of the 150 filmed flowers of *O. huajuapensis,* there were 107 instances with more than 1 bee on a flower at the same time, 9% involving individuals of *A. mellifera*. The presence of an *A. mellifera* and a *L. littoralis* male in the same flower occurred in 24% of the occasions but *A. mellifera* and *L. littoralis* females never shared the same flower. The coincidence of *L. littoralis* males and females in the same flower accounted for 43%, and pairs of *L. littoralis* males accounted for 23% of all the cases.

Agonistic behaviors on *O. huajuapensis* flowers occurred in all 107 instances where pairs of bees were recorded. Native males directed 55% of their agonistic behavior toward native females, 24% toward other native males, and 28% toward *A. mellifera*. Out of 26 agonistic events by *L. littoralis* males against *A. mellifera*, only 5 resulted in *A. mellifera* leaving the flower. When a pair of native males coincided, both flew away immediately from the flower and in only 1 instance did 1 of them, although it could have been another native male (we were unable to identify the individual), occupy the flower again. When a native male and a native female coincided, the male would bite the thorax of the female, but the female would remain feeding in the flower.

Discussion

We evaluated the feeding and agonistic behavior of *A. mellifera* and *L. littoralis* males and females on *O. huajuapensis* flowers, the first

Table 2. Bee numbers and corresponding percentages of behaviors displayed on *Opuntia huajuapensis* flowers by *Apis mellifera* and by *Lithurgus littoralis* males and females according to the behavioral group. Because we recorded only the first behavioral event, the numbers of bees per behavioral group were considered to be independent events.

Behavioral group	Bee count (n)	*A. mellifera* (%)	*L. littoralis* ♀ (%)	*L. littoralis* ♂ (%)
Floral visit	63	2.3*	6.3*	0.6
Feeding	103*	12.0*	0.6*	2.3
Exploratory flights	287*	3.0*	1.5*	38.0*
Walk on flower	42	0.1	0.1	5.8
Body cleaning	60	0.1	0.1	8.4*
Agonistic behavior	100*	0.1	0.1	14.6*
Inactive	24	0.0	0.6*	2.9
Rapid movement of abdomen	2	0.0	0.1	0.1
Proboscis exhibition	3	0.1	0.1	0.1
Column %		17.7	9.5	72.8

Asterisks indicate the 3 highest values within each column.

study of its kind on the relationship between these species. We found that agonistic behavior between *L. littoralis* males was more frequent when they were in the same flower with *L. littoralis* females, but there was no displacement. The displacement of *A. mellifera* was rare, but it occurred when 2 native males were on or near the same flower.

BEHAVIORAL REPERTOIRES

The Clench model allowed us to show that the behavioral repertoire of *L. littoralis* males was far richer (as shown by a higher asymptote) than that of the similar repertoire of *L. littoralis* and *A. mellifera* females, with most of their activities consisting of floral visits, collection of floral resources and exploratory flights, similar to other megachilid female bees (McKinney & Park 2012). The behavioral repertoire of *L. littoralis* males was more diverse. It included exploratory flights, which would allow them to assess the presence of other bees on flower resources. These males also displayed a larger proportion of agonistic behaviors compared with *L. littoralis* and *A. mellifera* females, including up to 7 different behaviors exhibited when coping with other bees on the same flower.

In most species of Megachilidae, males and females have different foraging strategies. Males take no part in cell provisioning or brood care and feed only to maintain their ability to copulate (Johnson & Hubbell 1974; Alcock et al. 1977; Eickwort 1977). This would explain the greater time spent by *L. littoralis* males in short flights and agonistic behavior, possibly as a strategy to compete with other males for access to females. In contrast, females need the energy to fly, to invest resources in eggs (Stone 1995), and to provision them with resources far beyond their own metabolic requirements. Therefore, females invest more time feeding than males, and their behavioral repertoire should allow them to optimize search patterns to obtain floral resources.

BEHAVIORAL RESPONSES

The behaviors performed by *A. mellifera* and *L. littoralis* in the flowers of *O. huajuapensis* varied among individuals. Our data show that 70% of *A. mellifera* fed only on nectar and that 16% performed exploratory flights that allowed them to distinguish flower characteristics and to evaluate resources (Townsend-Mehler et al. 2011). The flight over flowers performed by *L. littoralis* females would allow them to assess floral traits and resource availability and to avoid native males as reported for *Anthophora plumipes* Pallas (Hymenoptera: Apidae) by Stone (1995). This contrasts with the short exploratory flights exhibited by males, possibly a strategy to find females and to drive away other bees from their territory.

There was no evidence of agonistic behavior against conspecific or heterospecific bees by *A. mellifera* when visiting *O. huajuapensis* flowers, a behavioral pattern reported in other environments (Schaffer et al. 1983; Huryn 1997; Campos-Jiménez et al. 2014). Nevertheless, the feeding time spent by *A. mellifera* could lead to resource depletion and

Table 3. Time (s) and corresponding percentage of the behaviors displayed on *Opuntia huajuapensis* flowers by *Apis mellifera* and by *Lithurgus littoralis* males and females based on data extracted from 150 three-min videos. Because we recorded only the first behavioral event, the numbers of bees per behavioral group were considered as independent events.

Behavioral group	Time count (s)	*A. mellifera* (%)	*L. littoralis* ♀ (%)	*L. littoralis* ♂ (%)
Floral visit	375	1.05	0.40	1.08
Feeding	8,908*	39.67*	16.93*	3.49*
Exploratory flights	654*	1.93*	0.07	2.41*
Walk in the flower	388	2.24*	0.06	0.32
Body cleaning	640	0.95	1.44*	1.92
Agonistic behaviors	237	0.01	0.05	1.53
No activity	3,180*	0.00	6.79*	14.52*
Rapid movement of abdomen	166	0.00	0.02	1.10
Proboscis exhibition	295	0.18	0.16	1.65

Total recording time = 7.5 h, with bee activity = 4.1 h, without bee activity = 3.4 h
Asterisks indicate the 3 highest values within each column.

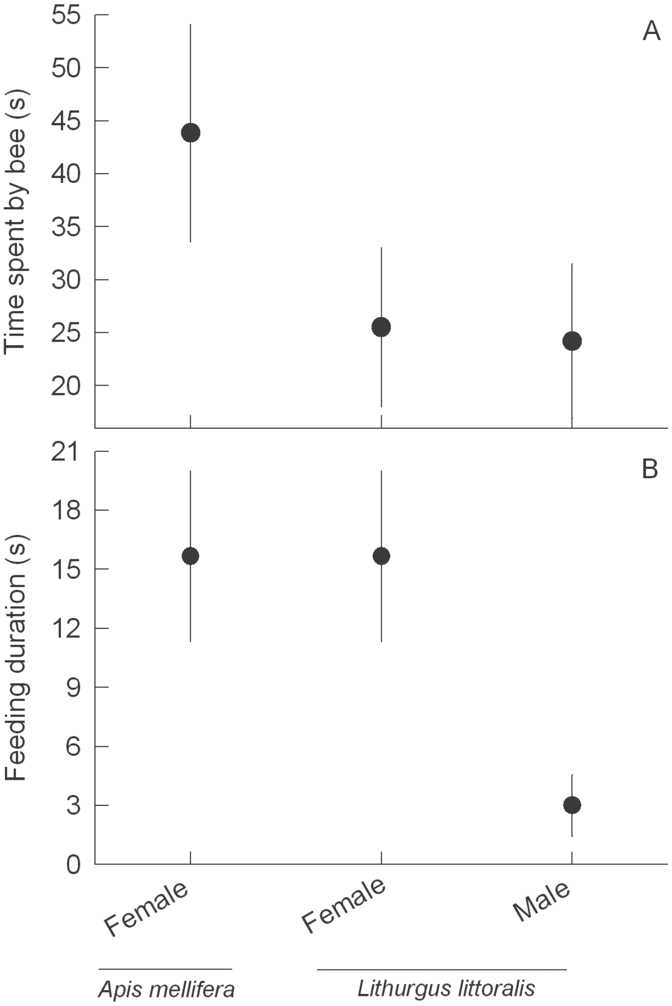

Fig. 2. Time spent (A) and mean feeding duration (B) in flowers of *Opuntia huajuapensis* by *Apis mellifera* females and *Lithurgus littoralis* females and males. No *A. mellifera* males were recorded at any time during the experiment. Vertical bars indicate 95% confidence intervals.

interference competition against native bees (Polatto & Chaud-Netto 2013). Such an extensive use of resources may give *A. mellifera* a competitive edge against other species (Schaffer et al. 1979; Paini 2004).

The lack of intraspecific agonistic behaviors of *A. mellifera* observed in our study could be a consequence of colony-specific identity by the mixture of chemical compounds that are carried on the surfaces of all workers and allow discrimination between self and non-self (Breed et al. 1995).

Males of *L. littoralis* were as aggressive as other oligolectic bees (e.g., *Ptilothrix fructifera* Holmberg [Hymenoptera: Apidae]; Oliveira & Schlindwein 2010) and megachilid bee species (Seidelmann 1999). We assume that the agonistic behavior between native males allows them to monopolize floral resources (Nagamitsu & Inoue 1997; Rivera-Marchand et al. 2008) and to compete for females (Alcock et al. 1978; Oliveira & Schlindwein 2010). The large proportion of male attacks toward females was consistent with previous observations on solitary bees (Stone 1995) in which agonistic behavior allowed males to drive away receptive females from the flower to copulate with them at ground level or to drive off gravid females in favor of receptive females.

The presence of immobile native male bees on cactus flowers seems to be a guarding behavior, as reported for the oligolectic bee *Diadasia rinconis* Cockerell (Hymenoptera: Apidae; Ordway 1987). This behavior likely functions as a means of interference competition, preventing the male from investing energy in direct confrontations with other males. This would involve a trade-off, as the male would reduce its risk and energy expenditure against opponents by reducing feeding time, which is short according to our records. Agonistic bees often benefit by having continuous access to the resource in contrast to passive bee species (Roubik et al. 1986), but this did not seem to be the case in the *L. littoralis* males because they spent little time on nectar consumption.

INTERACTIONS BETWEEN SPECIES

Apis mellifera individuals do not respond to the aggression of *L. littoralis* males, as reported when *A. mellifera* and *Trigona corvina* Cockerell (Hymenoptera: Apidae) interact (Roubik 1981). Our findings differ from those in which native species avoid the flowers when *A. mellifera* displays constant aggression towards them (Pinkus-Rendon et al. 2005). About 15% of native males attacked other bees during short intervals to drive them away from cactus flowers. In contrast, female native bees did not visit flowers if *A. mellifera* was present, possibly because the flower resources have been depleted, making their visit unprofitable. It is important to determine whether *A. mellifera* reduces resource availability such that it affects the feeding behavior and survival of *L. littoralis*, as reported for other native bees (Horskins & Turner 1999; Thomson 2004), or if it only reduces the reproductive success of the plant without compromising the fitness of native bees (do Carmo et al. 2004).

The behavioral repertoire of *A. mellifera* is less diverse than that of *L. littoralis* males. However, exploratory flights and feeding of *A. mellifera* and *L. littoralis* females are the dominant behaviors, likely due to their role in the collection of floral resources. We found that a large proportion of male bees displayed brief episodes of agonistic behavior and invested more time on defensive behavior against other bees, possibly as a strategy to increase access to receptive females on the flowers of *O. huajuapensis*

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