

## ON THE NESTING BIOLOGY AND CLEPTOLECTIC BEHAVIOR OF A NEOTROPICAL BEE, *PTILOTHRIX PLUMATA* SMITH, 1853 (HYMENOPTERA, ANTHOPHILA, EMPHORINI) IN AN ECOTONAL HOTSPOT OF SAVANNA IN THE “CERRADO” OF PARANÁ STATE (BRAZIL)

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**Abstract:** Nesting biology of *Ptilothrix plumata* Smith, 1853, including nest building behavior and cleptolectic interactions of females of neighboring nests, in the Cachoeira Farm lands, 12 km south-west of Jaguariaíva city (Paraná, southern Brazil). Evidence of use of water deposits (accumulation formed by night dew or rain) from *Peltaea edouardii* corolla to soften the moderately hard soil of the termite (*Cornitermes bequaerti* Emerson, 1952) mound walls serving as nesting substrate for the bee is mentioned. The possible influence of the females' cleptobiotic interaction as the cause of the unusual position of the egg (underneath the pollen provision) is also briefly discussed. Finally a brief comment on the role of the water accumulated in the corolla of the flowers of the principal (*P. edouardii*) source of pollen for *P. plumata* on pollination of the plant is made. The role of the cleptolectic behavior as a possible cause of distortion in reproductive success of the females, since we found a high proportion of provisioned cells with no eggs in them is also discussed.

**Key words:** Hymenoptera, Anthophila, Emphorini, *Ptilothrix plumata*, nesting biology, cleptolectic behavior, ecotonal cerrado (savanna), Brazil.

**Sobre el comportamiento nidificador y conducta cleptoláctica de una abeja neotropical, *Ptilothrix plumata* Smith, 1853 (Hymenoptera, Anthophila, Emphorini) en un enclave ecotonal de sabana situado en el “cerrado” del estado de Paraná (Brasil)**

**Resumen:** Comportamiento nidificador de *Ptilothrix plumata* Smith, 1853, incluido el comportamiento de construcción del nido y las interacciones cleptoléticas de las hembras de nidos vecinos, en los terrenos de la granja Cachoeira, 12 km al suroeste de la ciudad de Jaguariaíva (Paraná, Brasil meridional). Se ha constatado que la abeja usa los depósitos de agua (acumulaciones debidas al rocío o la lluvia) de la corola de *Peltaea edouardii* para ablandar el relativamente duro suelo de las paredes del termitero (*Cornitermes bequaerti* Emerson, 1952) que usa como sustrato de nidificación. Se discute brevemente la posible influencia de la interacción cleptobiótica de las hembras como causa de la inusual posición del huevo (bajo el polen acumulado en el nido). Finalmente, se hace un breve comentario sobre el papel que en la polinización de *P. edouardii*, principal fuente de polen de *P. plumata*, puede tener la acumulación de agua en su corola. Se discute también el papel de la cleptolectia como posible factor negativo en el éxito reproductor de las hembras, teniendo en cuenta que un alto porcentaje de las celdas aprovisionadas observadas no contenían huevos.

**Palabras clave:** Hymenoptera, Anthophila, Emphorini, *Ptilothrix plumata*, comportamiento nidificador, cleptolectia, cerrado (sabana) ecotonal, Brasil.

### Introduction

During the field phase of a long term ecological and biogeographical study of the wild bee communities in ecotonal sites of “cerrado” (savanna) of the northeastern region of Paraná [Sengés-Jaguariaíva (Paraná, Brazil) region], we had the opportunity to study nests of some species of wild bees. Recently, one of us (MCA) found two aggregations of nests of *Ptilothrix plumata* Smith, 1853, an oligolectic species foraging in the area exclusively on *Peltaea edouardii* (Hochreutiner) Kapovickas et Cristóbal, in the walls of two occupied termite mounds of *Cornitermes bequaerti* Emerson, 1952 (Isoptera, Termitidae, Nasutiterminae). As the nesting biology of bees is an adequate subject in the search for adaptations which would have correlation with the survival of these organisms in the peculiar biotopes of this ecotonal vegetation of southern Brazil and, as several aspects of the behavior of this bee are not well known yet, our additional observations on this species are briefly reported. *P. plumata* is a member of the Melitominae, one of the anthophorid group whose species tend toward specialization

for pollen requirements [e.g., the specialization of *Melitoma segmentaria* (Fabricius, 1804) on the pollen of certain species of *Ipomoea* (see Camilo *et al.*, 1993)].

*P. plumata* is a medium sized bee, whose females are predominantly brown-ferruginous, with a well marked yellow hairy band on each of the metasomal terga. Herein we report our observations on its nesting site, substrate and nest construction behavior. We also present notes on interactions between the owners (females) of neighboring nests. Most of the new information we present is complementary to that of other authors, such as Ihering (1904), Strand (1909), Pickel (1928), Michener & Lange (1958) and Martins *et al.* (1994).

*P. plumata* is the most abundant of its congeners [*Ptilothrix relata* (Holmberg, 1903) and *Ptilothrix fructifera* (Holmberg, 1903) are the other two species] in the area, in spite of being one of the rarest in comparison with all the other species of wild bees collected in a census done over several years of collecting efforts.

**Table I.** Results of analysis (chemical and physical) of soil samples collected in the nesting substrate (walls of the nests of *Cornitermes bequaerti* Emerson, 1952) of *Ptilothrix plumata* Smith, 1853 and in the “cerrado” in the vicinity of the nests (ca. 10 cm from the mounds), approx. 12 km west of Jaguariaíva city (Paraná, southern Brazil), February 2000. // Resultados del análisis (químico y físico) de muestras de suelo tomadas en el sustrato de nidificación (paredes de los nidos de *Cornitermes bequaerti* Emerson, 1952) de *Ptilothrix plumata* Smith, 1853 y en el “cerrado” de las inmediaciones de los nidos (a unos 10 cm del termitero), a aproximadamente km al oeste de la ciudad de Jaguariaíva (Paraná, Brasil meridional), en febrero de 2000.

#### CHEMICAL ANALYSIS

Samples	PH CaCl <sub>2</sub>	Al <sup>+3</sup>	H + Al	Ca <sup>+2</sup> + Mg <sup>+2</sup>	Ca <sup>+2</sup>	K <sup>+</sup>	T	P G/dm <sup>3</sup>	C g/dm <sup>3</sup>	Ph SMP	V %
	cmol <sub>2</sub> /dm <sup>3</sup>										
Termite nest *	4.20	0.90	9.70	1.70	0.90	0.25	11.65	5.0	19.4	5.10	16.74
Adjacent soil**	4.30	0.60	5.40	0.70	0.40	0.28	6.38	2.0	11.5	5.90	15.36

#### PHYSICAL ANALYSIS

	Fine sand (%)	Rough sand (%)	Silt (%)	Clay (%)
Termite nest *	6	52	18	24
Adjacent soil**	22	44	16	18

\* Collected from the external walls of the termite mound // Material recogido en las paredes exteriores del termitero.

\*\* From the field, in the vicinity (ca. 10 cm from the mound) // Material recogido del suelo en las inmediaciones (a unos 10 cm del termitero). [Columnas: arena fina / arena gruesa / sedimento / arcilla.]

Analysis made at the Department of Soil, Universidade Federal do Paraná, Brazil // Análisis hecho en el Departamento de Suelos, Universidad Federal de Paraná, Brasil.

## Nesting Biology

**STUDY SITE** — The nests were found in the Cachoeira Farm (*Fazenda Cachoeira*) lands (belonging to Mr. José Xavier da Silva), 12 km west of Jaguariaíva city (Paraná, southern Brazil), in the vicinity of the Diamond (*Diamante*) River, but 250-300 m away from its banks. The Jaguariaíva region belongs to the “lower montane moist forest life zone” (Holdridge system). However its original vegetation was predominantly “cerrado”. The occurrence of this plant community in the Jaguariaíva region is unusual because it is in a warm temperate climate region with predominance of forests (*Floresta de Araucária*, a vegetation which is typical of southern Brazil, especially of Paraná state) and, in some areas, by prairies (*Campos Gerais do Paraná*, another formation characteristic of the first and second plateaux of Paraná state). Its altitude is about 900 m. General information on this interesting and complex region is given in Maack (1968), as well as in Laroca & Almeida (1994). The site at which we found the nests was a somewhat disturbed area of “cerrado”, a particularly rich mixture of species of herbs and shrubs created as a result of the removal of most trees (i.e., it is now an open field vegetation enriched with typical “cerrado” plant species). The predominant plants at the site were: many species of Asteraceae [e.g., *Vernonia* spp. (including *Vernonia westiniana*), *Eupatorium* spp., *Baccharis* spp., *Senecio brasiliensis*, *Aspilota setosa*, *Wedelia paludosa*, *Calea* spp.] as well as species of Myrtaceae (*Eugenia* spp., *Campomanesia alba* etc.), and Rubiaceae (*Borreria* spp., *Declieuxia* spp. and *Palicourea rigida*), several species of Solanaceae (*Solanum lycocarpum* and *Solanum sisymbirifolium*), Leguminosae (s. l.) (*Senna*, *Cassia*, *Crotalaria*, *Clitoria*, *Andira humilis*), Malpighiaceae (*Byrsonima intermedia* and *Byrsonima coccolobaefolia*) and a few species of Convolvulaceae (*Evolvulus* and *Ipomoea*) and Malvaceae [including *Peltaea edouardii* (Hochreutiner) Krapovickas et Cristóbal (Fig. 1)]. Physical and chemical

analyses of the soil (Table I) were made at the Department of Soil (Universidade Federal do Paraná, which performs routine analysis for agricultural purposes).

► **Fig. 1.** Flower of *Peltaea edouardii* (Hochreutiner) Krapovickas et Cristóbal (Malvaceae). // Flor de *Peltaea edouardii* (Hochreutiner) Krapovickas et Cristóbal (Malvaceae).

**Fig. 2.** Nest of *Cornitermes bequaerti* Emerson, 1952 (Isoptera, Termitidae, Nasutiterminae) with nest entrances of *Ptilothrix plumata* Smith, 1853, at an ecotonal site of “cerrado” at Cachoeira Farm, Jaguariaíva city, Paraná, southern Brazil. // Nido de *Cornitermes bequaerti* Emerson, 1952 (Isoptera, Termitidae, Nasutiterminae), con las entradas de los nidos de *Ptilothrix plumata* Smith, 1853, en una localidad ecotonal de “cerrado” en la granja Cachoeira, área de Jaguariaíva, Paraná, Brasil meridional.

**Fig. 3.** *Ptilothrix plumata* Smith, 1853: **A** – Nest (transversal view); **B** – Egg at the bottom of the cell and pollen mass; **C-D** – Female in an initial phase of building the nest; **E** – Female in a more advanced phase of nest building; **F** – Female closing the nest; **G** – Nest entrance with soil softened by liquid (possibly water); **H** – A closed nest with a female working inside it; **I** – Nest entrance with a turret; **J** – Nest definitively closed; **K** – Female closing the nest entrance with the distal part of her metasoma; **L** – Pollen load left by a stealing female (after completing her own pollen mass) at the entrance of the nest, later retaken by the robbed female. // *Ptilothrix plumata* Smith, 1853: **A** – Nido (vista transversal); **B** – Huevo en el fondo de la celda y masa de huevos; **C-D** – Hembra en la fase inicial de construcción del nido; **E** – Hembra en una etapa más avanzada de la construcción del nido; **F** – Hembra cerrando el nido; **G** – Entrada del nido y sustrato reblandecido con líquido (posiblemente agua); **H** – Nido cerrado con una hembra trabajando dentro; **I** – Entrada del nido con torreta; **J** – Nido definitivamente cerrado; **K** – Hembra cerrando la entrada del nido con la parte distal del metasoma; **L** – Carga de polen dejada por una hembra ladrona (después de completar su propia masa de polen) a la entrada del nido, más tarde recuperado por la hembra víctima del robo.





1



2



3

**NESTING SUBSTRATE AND DISTRIBUTION OF NESTS WITHIN THE AGGREGATION** — At the site there were a good number of termite nests. The two nests in whose walls the nests of *P. plumata* were found belong to *Cornitermes bequaerti* Emerson, 1952 (Isoptera, Termitidae, Nasutiterminae) (Fig. 2). These were the only two occupied nests of this termite in the whole area. There was one other, unoccupied nest of this species at the site, but it had no *P. plumata* nests. According to Dr. Luiz R. Fontes (personal communication), the nests of *C. bequaerti* generally have subterranean parts larger than the mound visible above the soil surface. The outer part of the nests we studied was approximately conical, with a basal diameter of 100 cm and a height of 50 cm. The nests were characterized by tunnel systems, some opening to the exterior by holes situated in the uppermost part, where the tunnels were circular or slightly elliptic in transverse section. This tunnel system keeps the innermost organic nucleus (as well as the walls where the bees nests were found) with the right climatic conditions. The analysis of soil samples from both the nests and near the termite nests gave the results shown in Table I.

Comparing the results of the analysis of termite nests' walls with those obtained in the analysis of the soil sample collected in the vicinity of the nests, we observe larger differences in H + Al,  $\text{Ca}^{+2} + \text{Mg}^{+2}$ ,  $\text{Ca}^{+2}$ , T, P and C. Relatively small differences were found between  $\text{Al}^{+3}$ ,  $\text{K}^{+}$  and V (%). The values of Ph ( $\text{CaCl}_2$ ) and Ph (SMT) are very similar.

The curves of retention values are similar, but a little (though consistently) higher in the termite nest walls, as follows: 11.9 and 11.2 (at 0.33 atm), 11.2 and 10.2 (at 1.0 atm), 9.1 and 8.6 (at 5.0 atm) and 9.9 and 9.6 (at 15.0 atm).

The soil is extremely acid and similar in several other respects to those of typical "cerrado" areas of the central region of Brazil (see Goodland & Ferri, 1979).

Both mounds of *C. bequaerti* had aggregations of about 40-50 nests of *P. plumata*. The bee nests on both mounds were aggregated at the eastern sides exposing them to direct morning sun. Since nests are simple, generally consisting of a small gallery with a vestibular area ending at a single cell (Fig. 3 A), when they are ready (*i. e.*, after the bee has laid in provisions and oviposited) they are closed. In the aggregations there are bee nests at several stages of construction, some unfinished and open and others closed (Fig. 3 C – J). We were able to take two series of measurements of distances between the nests, one including all the nests and the other only the open ones [in the series concerning the latter (only open), the measures were taken in October, 2000, when the nesting season was just beginning]. As the figures are few, and as they might be important in future comparisons, the raw data are listed below.

The distances (in cm) between the nearest nests (only open ones) in *termite mound number one* are as follows: 2.0, 2.5, 3.0, 4.0, 4.0, 6.0, 7.0, 8.0, 8.0, 8.0, 12.0. For these eleven values, the mean distance (with its standard error) is:  $5.86 \pm 0.92$  cm. The distance values (cm) (also open nests only) for *termite mound number 2* are: 1.0, 2.0, 2.5, 4.0, 4.0, 4.5, 4.5, 6.5, 6.5, 8.0, 8.0. The mean distance (with its standard error) is:  $4.68 \pm 0.71$  cm. The difference between the two series is not statistically significant (Man-Whitney non parametric U-test) [ $U (=72) < U_{0.05} (2, 11, 11, (= 91))$ ].

In the latter termite mound, in February, 2001, two other series of distances [open and open + closed (as a

whole)] (not only the nearest neighbors were considered) were taken, as listed below: open *nests*: 0.5, 0.5, 1.0, 1.0, 1.0, 1.0, 1.5, 1.5, 1.5, 1.5, 1.5, 1.5, 1.5, 1.8, 2.0, 2.0, 2.0, 2.0, 2.0, 2.3, 2.4, 2.5, 2.5, 2.5, 3.0, 3.5, 4.0, 4.0, 4.0, 4.0, 4.0, 4.3, 4.5, 4.5, 6.0, 6.5, 6.5, 7.0, 8.0, 8.0, 8.0, 8.0, 8.0, 12.0 cm. Mean (and standard deviation):  $3.62 \pm 0.55$  cm ( $n=43$ ). For the *open + closed* nests (as a whole) the measurements are: 0.5, 0.5, 1.0, 1.0, 1.5, 1.5, 1.5, 1.5, 1.5, 1.5, 1.8, 1.8, 2.0, 2.0, 2.0, 2.3, 2.4, 2.5, 3.5, 4.0, 4.5 cm. The mean distance is smaller than in the series in which the closed nests are not considered:  $1.89 \pm 0.21$  cm. Obviously, the difference between both series is statistically significant [ $|Z| > t_{0.05} (2)$ ], as expected.

**NEST CONSTRUCTION BEHAVIOR** — We observed nest construction by many females at both aggregations of nests of *P. plumata*. In some of those nests we observed the female building behavior from the initiation to the phase in which the cell was ready to receive the provisions (pollen) and the egg (Fig. 3 B - J). On January 30, 2000, we recorded the duration of the whole building process, which was about four hours (from 10 h 30 min to 14 h 30 min) (Fig. 4). The meteorological conditions during the behavioral observations were roughly as follows: clear sky, air temperature 21-24 °C, 64-70 % relative humidity, completely windless. Heavy rain had fallen the previous night (Jan. 29-30, 2000).

The nest building behavior for all observed nests consists of two kinds of activity: nest digging and field trips to find and collect liquid (we tasted humid soil clots removed from nests during the building process and they were as insipid as water, we assume that this liquid as water or perhaps a very diluted nectar). The bees were observed using liquid to soften the compact soil of the termite nest's external walls (Fig. 3 G). During this period of digging, the female made 35 field trips. The duration of such trips varied according to two main categories: one (29 trips) varying about 50 seconds ( $n = 26$ , mean =  $49.52 \pm 1.12$  seconds) and the other (9 trips) from 170 up to 524 seconds ( $n = 9$ , mean =  $249.44 \pm 35.76$  seconds). As a whole ( $n = 35$ ), the mean time per trip was  $147.58 \pm 48.52$  seconds. Figure 4 (Left, Above) shows the time of each successive field trip and that there is a very high degree of regularity in the distribution of the time spent in the successive field trips in order to collect liquid (water and/or nectar). The distribution (period between two successive trips) of time taken in excavation does not show any defined regularity (Fig. 4 Right, Above). To build the entire nest including the cell the female spent three hours and thirty-three minutes. Of this total duration, 58.6 % (two hours and five minutes) were spent in excavation activities and 41.4 % (one hour and twenty-eight minutes) in field activities (collecting water and/or nectar). The result of this approximately three and a half hour work was a nest 4 cm deep, including an empty cell 0.4 cm across, a short vestibule, as well as a short gallery and a turret 2-3 mm high (Fig. 3 I).

The regularity of time spent during liquid gathering activities the days after the rainy night is also shown in the graphs (Fig. 4, Top and Middle).

On November 17, 2000, we were able to repeat our observations with another bee from 0:55 min. p.m. to 3:00 p.m. (Fig. 4 Middle). The weather was roughly as follows: cloudy sky (eight parts out of ten covered), air temperature



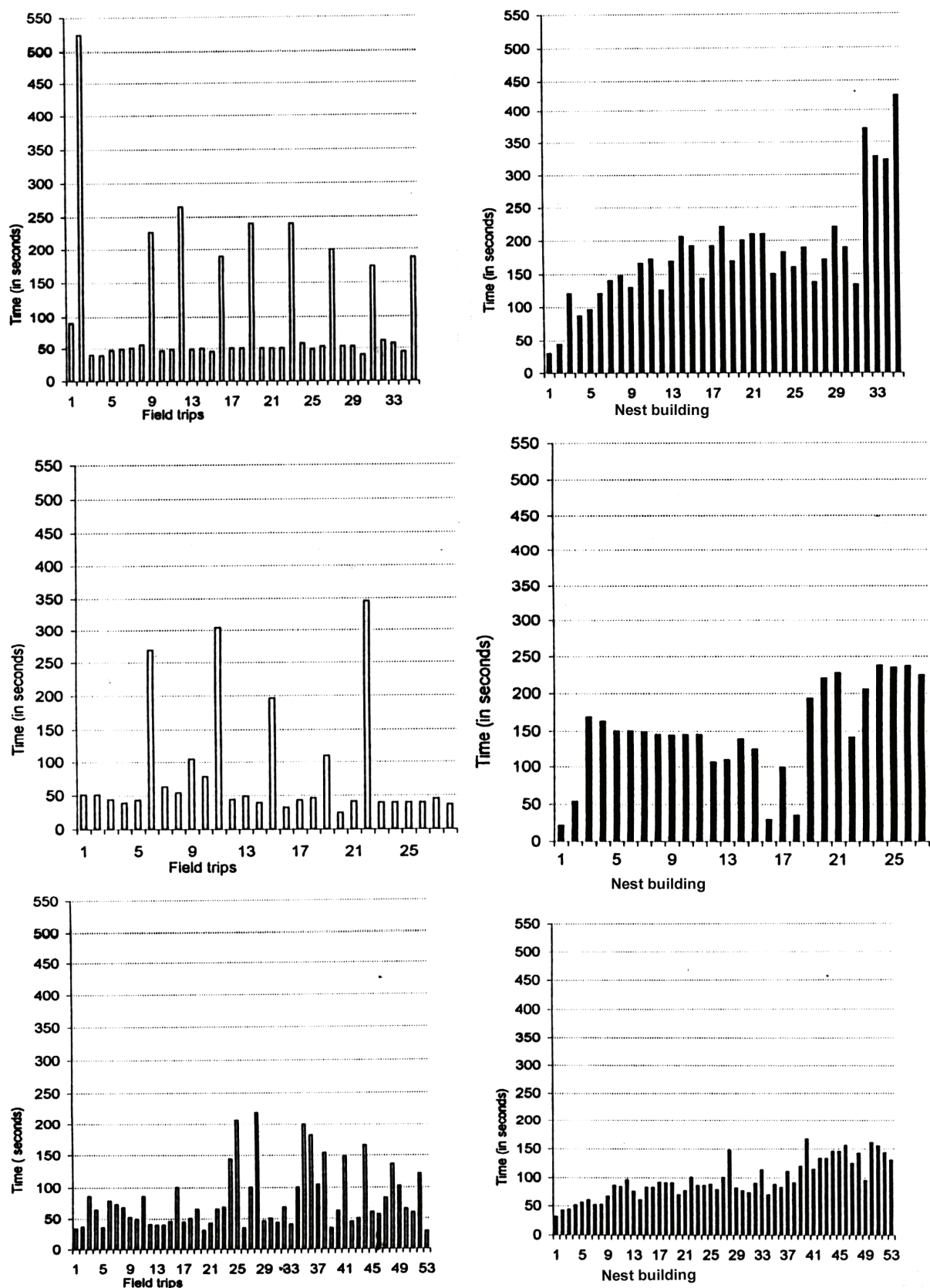


Fig. 4. *Ptilothrix plumata* Smith, 1853: left side – Time of successive field trips to find and collect liquid; right side – time devoted to nest building; top – January 30, 2000 (after a rainy night); middle – November 17, 2000 (after a rainy night); bottom – October 17, 2000 (with dried soil). // *Ptilothrix plumata* Smith, 1853: lado izquierdo – tiempos de las sucesivas salidas destinadas a la localización y recogida de líquido; lado derecho – tiempo dedicado a la construcción del nido; arriba – 30 de enero de 2000 (tras una noche lluviosa); centro – 17 de noviembre de 2000 (tras una noche lluviosa); abajo: 17 de octubre de 2000 (con el suelo seco).

21-24 °C, 71-74 % relative humidity, a moderate to calm wind. Heavy rain fell the previous night (Nov. 26-27, 2000). During our observations the female made 28 field trips (Fig. 4 Left, Middle). The time spent in the shortest trips varied from 24 to 78 seconds ( $n = 22$ , mean =  $44.45 \pm 2.33$  seconds) and for the longer trips it varied from 109 to 345 seconds ( $n = 6$ , mean =  $221.17 \pm 41.40$  seconds). As a whole ( $n = 28$ ), the average time per trip was  $82.32 \pm 16.52$  seconds. The nest building female spent a total of two hours and twenty-three minutes (Fig. 4 Right, Middle). Of this total, 73.20 % of the time was spent digging and 26.80 % in field trips.

There was also heavy rain during the night previous to March 28, 2001. This day, the behavior was watched for a shorter period, but nevertheless the regularity trend was also clearly visible. Weather conditions varied as follows: moderately cloudy (1/6 to 1/7 of the sky with clouds), moderate to high insolation, air temperature 23-27 °C, 67-98 % relative humidity, from completely calm (no wind) to moderately windy. For the short trips ( $n = 23$ ), the average time spent per trip was  $42.52 \pm 1.25$  seconds, while for the long ones ( $n = 4$ ), the average time per trip was  $249.50 \pm 55.57$  seconds. Out of a total of approximately one hour and twenty-two minutes, 59.90 % was spent in digging activities, while 41.1 % in liquid collecting activities.

Therefore in all three cases, the amount of time spent digging varied from 58.6 % to 73.20 % while liquid collection took from 26.80 % to 41.40 % of the time.

Unfortunately the observations were carried out during just one day on which the field was dry (there had been no rain the previous night), and this was in October 19, 2000. On this day there was a tendency to delay the period spent in field trips, as can be seen in the graph (Fig. 4 Top). From the total time, 58 % was spent in field trips, with just 42 % in digging activities. Comparing these results with those obtained on October 17, 2000, it is evident that under humid conditions the bees spent less time in outdoor activities (Fig. 4 Bottom).

### Flower visits and foraging behavior

The female bees of the aggregations we studied were collecting pollen only of *Peltaea edouardii* (Hochreutiner) Krapovickas et Cristóbal, and all the pollen provisions we extracted from nests were of this plant. The pollen masses within the individual cells of the nest were ferruginous, hemispheric and occupied about 2/3 of the space. The eggs we found were each beneath the pollen provision (as is normally reported for the Melitomini), rather than on top, which is the usual case in most species of bees (Fig. 3B).

The flowers of *P. edouardii* are open only in the morning (9 - 9:30 to 11:30 -12). Sometimes they become partially filled with rain or dew to up to about 1/5 of their volume. When that happens (as observed on November 27, 200 and March 3, 2001), pollen that is exposed loosely on the anthers can be dispersed in the water.

On the day when we observed female bee A, we measured the closest blooming plant of *P. edouardii* at about 2 m from the nest, and the furthest at about 50 m. Within that radius there were about 25 blooming plants. The array of values for the time (in seconds) spent in the field and at the nest (values inside the parentheses) to unload the

pollen load was the following: trips — 1: 300 (30), 2: 93 (60), 3: 150 (32), 4: 314 (35), 5: 32 (18), 6: 211 (42), 7: 350 (29), 8: 175 (45), 9: 120 (43), 10: 205 (658), 11: 263 (39), 12: 323 (60), 13: 80 (17), 14: 45 (35) and 15: 128 (39). The time spent in the field varied from 32 to 350 seconds ( $n = 15$ , mean =  $185.93 \pm 27.13$  seconds) and inside the nest the duration varied (the value 658 was not considered) from 17 to 60 seconds ( $n = 14$ , mean =  $37.43 \pm 3.39$  seconds).

### Cleptoleptic behavior

These records were taken on January 25, 2000 at *termite mound number 2*, between approximately 10 h 5 min. and 11 h 30 min. a.m., with 27-28 °C, 65 % relative humidity and a 2 m/s north-east wind, on a clear day. On one occasion we observed that in a very short period of time (approximately eight minutes) a single female came to her nest on four successive trips carrying in her scopal hairs a full load of pure *P. edouardii* pollen. We were astonished with this phenomenon since, by our assumption, it would be impossible for the female to gather the pollen loads directly on the flowers in such a short period of time. In fact, previously we had recorded in our field notebook the expression “*high promiscuity*” in reference to the behavior of the females, since we had registered also “relatively common rapid visits of these individuals in the neighboring nests belonging to other owners (females of the same species)”. However, the most interesting instances of these crude interactions between two females, took place between the owners of two neighboring nests, which we referred to as *female number one* and *female number two*. At first, *female number one* went to the nest of *female number two* in a very short period of time and got two complete loads of pollen, which were unloaded in her own nest. Later she left her own domicile, then *female number two* took twelve trips to nest *number one* and on each of these trips carried a full load of pollen to her own nest. On the 5<sup>th</sup> trip she lost approximately 1/3 of the pollen load of one of her hind legs, which fell on the termite mound’s surface. After finishing one of her successive trips, she retrieved the portion of pollen that had fallen on the mound’s surface. In the course of her 14<sup>th</sup> trip, when the owner had returned to the nest, there was an apparent violent struggle with the owner and she was chased away, getting back to her own nest. Once in the nest she positioned herself near the entrance in an apparent readiness posture (head up and antennae erect). The other female remained in her own domicile in a similar attitude. On this occasion, our observations in the vicinity of the nest lasted approximately twenty-five minutes and during this period the bees remained in the guard posture at the nest entrance.

On November 26, 2000 [74-95 % relative humidity, 18-21,5 °C, insolation high, wind about 3 km/hour], the behavior of two other females while visiting *P. edouardii* flowers was observed and recorded. It is a very rapid process lasting about 10-15 seconds, consisting of walking in the transverse direction on the floral stamens and integrating the loose pollen grains in their scopae.

Another interesting set of interactions were observed on March 19, 2001 [9:45 a.m., 26 °C, 65 % relative humidity, wind: 3 (Beaufort scale), cloudy] (Table II). On this day, one female (A) brought to her nest fifteen complete loads of pollen harvested on the flowers of *P. edouardii*. The foraging

**Table II.** Interactions between two *Ptilothrix plumata* females, owners of two neighboring nests, in the “cerrado” (savanna) region of Jaguariá (Paraná state, Brazil), October 19, 2000. // Interacciones entre dos hembras de *Ptilothrix plumata*, propietarias de dos nidos vecinos, en la región de “cerrado” (sabana) de Jaguariá (estado de Paraná, Brasil) el 19 de octubre de 2000.

Event number	Time	Invader	Invaded nest	Time in the invaded nest or in the field	Time spent to deposit pollen	Behavior & results
1	10:00 a.m.	Female A	-	-	A few seconds	<i>A moderate pollen load.</i>
2	10:05 a.m.	Female A	-	4 min 55 seconds	A few seconds	Once in her nest, the female remained for a while with her antennae pointing upward to the entrance hole. <i>A moderate pollen load.</i>
3	10:22 a.m.	Female A	-	A few seconds	A few seconds	Remained for a while in her nest. <i>A moderate pollen load.</i>
4	10:24 a.m.	Female A	-	A few seconds	A few seconds	Female invaded rapidly two nests, then disappeared for approx. 4 min. from our sight. Pollen possibly collected in the field. <i>A small pollen load.</i>
5	10:30 a. m.	Female A	-	A few seconds	A few seconds	Female left her own nest for unknown destination. <i>No pollen.</i>
6	10:30:30 a. m.	Female B	Nest A (owner absent)	10-15 seconds	A few seconds	No antagonistic interaction. <i>A large pollen load.</i>
7	10:31 a. m.	Female B	Nest A (owner absent)	15 seconds	A few seconds	No agonistic interaction. <i>A large pollen load.</i>
8	10:32 a. m.	Female B	-	2 min 20 seconds	-	Possibly trip to the field. <i>No pollen.</i>
9	10:35 a. m.	Female B	-	-	-	Left her own nest.
10	10:37 a. m.	Female A	Nest B (owner absent)	A few seconds	A few seconds	<i>A large pollen load.</i>
11	10:38 a. m.	Female A	Nest B (owner absent)	A few seconds	A few seconds	<i>A large pollen load.</i>
12	10:38:30 a. m.	Female A	Nest B (owner absent)	A few seconds	A few seconds	<i>A large pollen load.</i>
13	10:39 a. m.	Female A	Nest B (owner absent)	11 seconds	A few seconds	<i>A large pollen load.</i>
14	10:39:30 a. m.	Female A	Nest B (owner absent)	A few seconds	A few seconds	<i>A large pollen load.</i>
15	10:40 a. m.	Female A	Nest B (owner absent)	8 seconds	A few seconds	<i>A large pollen load.</i>
16	10:40:20 a. m.	Female A	Nest B (owner absent)	10 seconds	A few seconds	<i>A large pollen load.</i>
17	10:40:40 a. m.	Female A	Nest B (owner absent)	11 seconds	A few seconds	<i>A large pollen load.</i>
18	10:41 a. m.	Female A	Nest B (owner absent)	10 seconds	A few seconds	<i>A large pollen load.</i>
19	10:41: 20 a. m.	Female A	Nest B (owner absent)	-	-	<i>No pollen.</i>
20	10:41:30 a. m.	Female A	-	-	-	Intense work in her own nest – egg laying, molding the pollen supply and closing the cell. A certain quantity of pollen left in the gallery, near the entrance (Fig. 3 L).
21	10:46 a. m.	Female B	Nest A (owner present)	A few seconds	A few seconds	No antagonistic interaction. <i>A large pollen load.</i>
22	10:46:20 a. m.	Female B	Nest A (owner present)	A few seconds	A few seconds	No antagonistic interaction. <i>A large pollen load.</i>
23	10:46: 40 a. m.	Female B	Nest A (owner present)	A few seconds	A few seconds	No antagonistic interaction. <i>A large pollen load.</i>
24	10:47 a. m.	Female B	Nest A (owner present)	30 seconds	A few seconds	No antagonistic interaction. <i>A large pollen load.</i>
25	10:47:10 a. m.	Female B	Nest A (owner present)	A few seconds	A few seconds	No antagonistic interaction. Nothing
26	10:48 a. m.	Female A	-	40 seconds	-	Female left her nest. Possibly a portion of liquid.

**Remarks** – From about 10:42 a. m. to 11:42 a. m. female A worked closing her own nest, with periodic field trips to collect liquid. At 11:43 a.m. female B attempted to invade nest A, but it was already closed. At twelve o'clock the observations of these two nests were interrupted. // **Comentarios:** Desde alrededor de las 10:42 a. m. hasta las 11:42, la hembra A trabajó en el cierre de su propio nido, con desplazamientos periódicos para recolectar líquido. A las 11:43 la hembra B intentó invadir el nido A, pero ya estaba cerrado. A las 12:00 se interrumpió la observación de estos dos nidos.

activities this day lasted until 11:30 a.m. At this time, there was virtually no pollen on the flowers in the immediate surroundings, and a large number of the blooms were nearly closed. At 11:30 a.m., in the absence of the owner, the female from neighboring nest (B) entered nest (A) and got three complete pollen loads. In the course of the fourth trip, when she was trying to get more pollen, she came across the owner inside her own nest and was not able to enter. After five attempts to get into the nest, she was driven off by the owner, who then closed the nest with the distal part of her abdomen (Fig. 3 K).

## Final comments

The results presented in this work have raised some interesting questions on the nesting biology of *P. plumata*, especially on the source of water used to soften the soil serving as nesting substrate, in the present case the moderately hard soil of the walls of the nests of *C. bequaerti*. As has been shown (Fig. 4) the time spent by a female in the field trips for this purpose was insufficient to reach the only normal source of water (the Diamond river, distant 250-300 m from the nest aggregations); so, instead they probably use water found in the corolla (accumulation from the night dew and/or precipitation) of several flowers, including the ones of the visited plant of the present oligolectic species. In our multi-annual census of bee communities in Jaguariaíva-Sengés “cerrado” region we have collected females of this species on the flowers of *P. edouardii*, some of them with dew or rain water accumulations at their bottoms, such as the ones seen in Figure 1. This phenomenon was observed frequently during the rainy months (January and February). This fact and the regularity pattern of time distribution in field trips for water gathering during the process of nest building, indicate that the sources of water in the area are the corollas of *P. edouardii*. If this hypothesis is correct then one of the next problems to be explained is the role of this process in the pollination of this plant, since we found high concentrations of pollen grains in these floral deposits of water. It seems also interesting to establish the relationships between the position of the eggs in the cells, which may be on top of (as is usual in the vast majority of bee species) or underneath the pollen mass (see Martins *et al.*, 1994), and the cleptolectic interaction [a phenomenon discovered by Laroca in *Apis* (cf. Laroca & Winston, 1978) and labeled as *cleptolectic behavior* by Thorp & Briggles (1980)]. A plausible hypothesis is that the egg location in this species is an evolutionary consequence of the intensity of the cleptolectic interactions taking place at sites like these. Finally, it seems worthwhile to emphasize that the records indicate that *P. plumata* in this ecotonal area of “cerrado” is not a multivoltine species (as observed by Martins *et al.*, 1994) but bivoltine. The question of whether this is or is not a biogeographical trend is a problem to be solved in the future in a larger scale, deeper study. Another phenomenon that seems worth investigating in depth is the fact that, as the result of the cleptolectic interactions between neighbor females, a relatively high percentage of nests end up provisioned but without any eggs being laid in them, which perhaps explains why a high percentage of cells are found with the pollen supply attacked by fungi.

This fact also has sociobiological and evolutionary consequences, since the interactions cause a reproductive “distortion”, decreasing the chance of some females leaving descendants. It seems interesting to emphasize that the populations of *P. plumata* studied in the present work were very aggregated and therefore possibly had a high inbreeding coefficient and a clear superposition of females of different ages, with the older females (perhaps mothers) being the most experienced individuals and having a higher chance to dominate the others and to lay more eggs than subordinate females.

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