

Run to the nest: A parody on the Iron Maiden song by *Corotoca* spp. (Coleoptera, Staphylinidae)

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Abstract. Rove beetles belonging to the genus *Corotoca* (Staphylinidae: Aleocharinae) are termitophiles exclusively found in nests of *Constrictotermes* (Isoptera: Termitidae). We observed the reproductive behavior of *Corotoca melantho* and *C. fontesi* during host (*Constrictotermes cyphergaster*) foraging events. The reproductive behaviors of both species are similar. The variables collected for analysis were distance traveled, the time of larval deposition, nest return time, and locomotion speed. The fact that the female stops in the middle of the foraging trail to deposit the larva leads to a discussion of how its physiological or voluntary mechanisms function to determine the correct stopping time and the importance of speed when returning to the nest as a strategy to avoid predation. This study provides new information concerning the life cycle of *Corotoca* spp., although complete understanding of host-termitophile relationships, their evolutionary history, and the significance of viviparity will require additional studies.

Key-Words. Passive dispersal; Termite; Rove beetle; Termitophily.

INTRODUCTION

Active termite nests commonly house diverse species of rove beetles of the family Staphylinidae. The subfamily Aleocharinae is by far the most successful group of guests in termite nests (Seevers, 1957; Kistner, 1969; Cristaldo *et al.*, 2012), and although those species are commonly found inside the nests, information concerning their ecology and behavior is still quite scarce (Kistner, 1969; Jacobson *et al.*, 1986).

Termitophily has evolved several times among aleocharine rove beetles, and includes a wide range of morphologically specialized organisms. That habit emerged at least 99 mya, with fossil of extinct termitophilous Trichopseniini species known from mid-Cretaceous Burmese amber (Cai *et al.*, 2017). Termitophylous clades have arisen at least 11 times in the subfamily Aleocharinae, with over 650 described species displaying a series of adaptations to either bribe or trick their hosts (Grassé, 1997; Kanao *et al.*, 2016; Rosa *et al.*, 2018). Two morphological adaptations have evolved: the inconspicuous horseshoe-shaped forebody

form of the limuloid, and the large, conspicuous physogastric forms (Seevers, 1957). As discussed by Cristaldo *et al.* (2012), the limuloid body tends to minimize interactions with termite and maximize the hiding capabilities of the intruder species, while physogastric body forms maximize interactions with the termites and facilitate social integration. That view is corroborated by research on the origin of termitophily in Aleocharinae (Kanao *et al.*, 2016) and their multiple interactions with their hosts (Grassé, 1997; Kistner, 1969).

Among the physogastric Aleocharinae, the pantropical tribe Corotocini contains the most specialized termitophilous organisms, and more than described 200 species. The tribe possibly evolved early within Nasutitermitinae, diversifying over a long period of time (rather than by frequent host transfers) (Jacobson *et al.*, 1986). The genus *Corotoca* Schiødte 1853 comprises some of the most morphologically modified flightless and viviparous corotocine beetles with highly developed physogastric abdomens occurring since the first records of other animals living in association with termites (Schiødte, 1853). Those beetles are

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found only in association with the genus *Constrictotermes* Holmgren, 1910 (Isoptera: Termitidae) (Seevers, 1957), a genus found in evergreen and dry forests throughout South America (Cunha *et al.*, 2006; Vasconcellos *et al.*, 2010). It is not entirely clear how *Corotoca* species feed, although trophallaxis is probably involved (as evidenced by the reduction of the mouthparts in species of that genus) (Seevers, 1957; Zilberman, 2018b). The beetles also demonstrate general morphometric similarity to the host workers (Cunha *et al.*, 2015), as has been reported for other termitophiles, and those inquilines also produce mimetic cuticular hydrocarbons (Rosa *et al.*, 2018).

The larvae of the *Corotoca* females develop in their greatly enlarged abdomens (see Zilberman, 2018a: figs. 1, 2) and Seevers (1957) hypothesized that the larvae would pupate almost immediately after release as they "are released in an advanced stage". Seevers (*l. c.*) also noted that no larvae had yet been found inside termite nests, and Oliveira *et al.* (2018) reported that adult females of the genus *Corotoca* visit termite foraging trails in order to deposit larvae.

Dispersing larval instars is uncommon among terrestrial invertebrates (Strathmann, 1990), and the process in which the animals are dispersed without energetic expense is called passive dispersal. That is the case with of dipterous species that are transported by birds (Green & Sánchez, 2006), and gypsy moths that

are transported by the wind (Mcmanus & Mason, 1983). What makes *Corotoca* spp. dispersal so intriguing is the fact that the larvae are transported by workers along a foraging trail (Oliveira *et al.*, 2018). Phoresy between adult Aleocharinae and termite hosts is not uncommon (Kistner, 1969), although the significance of that behavior to the inquiline species is still unclear and using foraging as a dispersal vehicle of phoretic behavior is even more intriguing.

We collected data on the reproductive behavior of *Corotoca* spp. (the distance traveled, time until stopping for depositing the larvae, and time required for returning to nest) in a semiarid region of Brazil in an attempt to discover how behavioral variables interact and shape that phenomenon.

MATERIALS AND METHODS

Sample site

Data were collected at the São João do Cariri Experimental Station (EESJC) (Fig. 1) in Paraíba State, Brazil. The station is managed by the Federal University of Paraíba, and is located in Cariri of Paraíba. The regional environment is dominated by dry forest and well-spaced shrubby Caatinga vegetation (Bucher, 1982); the climate

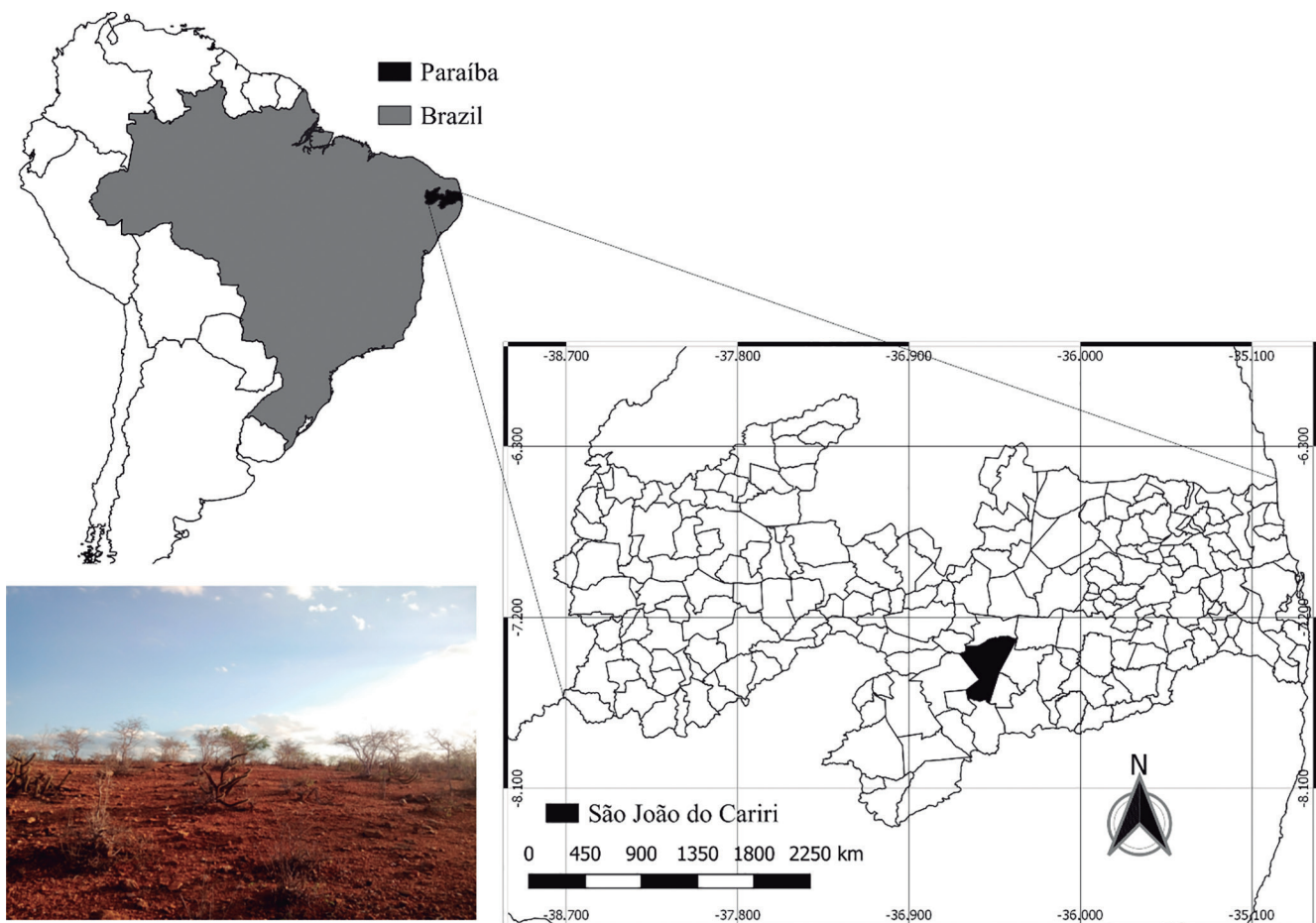


Figure 1. São João do Cariri Experimental Station (ESSJC). The station is located in a semiarid environment with some ongoing processes of desertification. Efforts are currently being made to aid the recovery of the local fauna and flora.

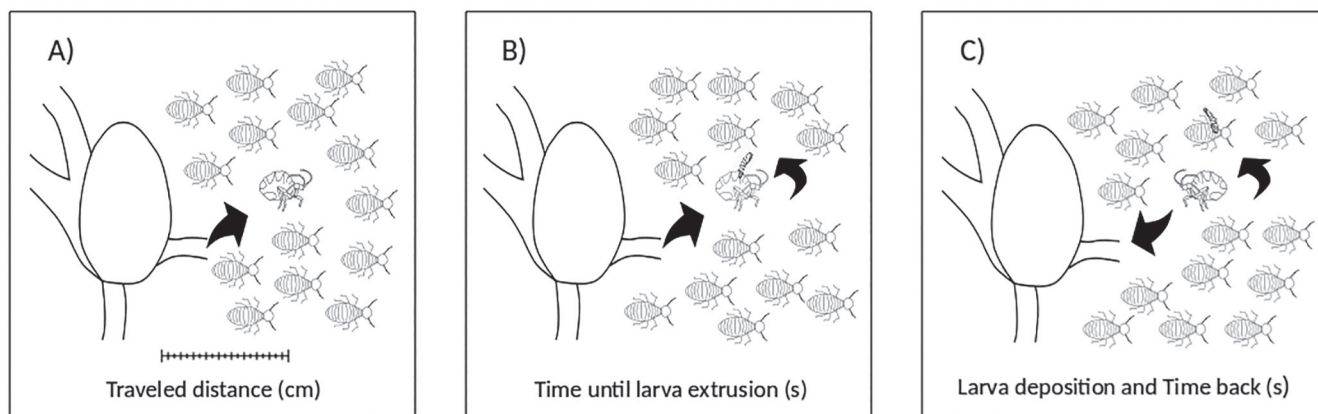


Figure 2. Scheme of the collection methodology: (A) *Corotoca* spp. leaves the nest to follow the host foraging trail. It is closely observed until stopping; the distance from the nest to where the beetle stops is measured and the time required is recorded; (B) When the beetle stops, the stopwatch is paused while larval extrusion occurs; (C) After larval the position, the return time of the beetle to the nest is recorded.

is semiarid and hot, the rainfall rates there are the lowest in the Brazilian semiarid region, annual mean precipitation is below 400 mm (Cohen & Duqué, 2001), and the mean annual temperature is 26°C (Barbosa et al., 2007).

Data collection

Field excursions were undertaken in November/2017 and in January/2018. The foraging trails of five nests of *Constrictotermes cyphergaster* were monitored and data on the reproductive behavior of *Corotoca* spp. (n = 24) was collected (12 specimens of each species), noting the time when foraging initiated and when each beetle left the nest. We measured the distances traveled (using a tape measure, in cm), the time until larval extrusion, and the time required for returning to the nest (using a stopwatch) – with pauses during the process of larval deposition (Oliveira et al., 2018) (Fig. 2). The beetles were collected using a thin forceps as soon as they returned to the entrance of the nest. Collecting beetles from the trails naturally caused disturbances of its flow, so that intervals of at least five minutes were respected after each collection before restarting monitoring. The egression speed of the beetles was calculated by dividing the time until stopping by the distance traveled (V1); the regression speed was calculated by noting the time required to return to the nest (V2).

The collected specimens were identified (*Corotoca melantho* and *C. fontesi*) using the key provided in Zilberman (2018b). Voucher specimens were deposited in the Termite Ecology Laboratory at the State University of Paraíba.

Data analysis

We tested the normality of data collected using visual analyses of density and the Shapiro-Wilk test. Some of the variables failed to satisfy the requirements of normality (Time until stopping (P < 0.01) and V1 (P < 0.001)). We tested the homogeneity of the errors of the normal

variables using Bartlett’s test (all P > 0.05). The Student’s T tests was performed using species as factors (x-var) in order to determine if there were differences between the species.

The speeds of the beetles were compared (V1 against V2) using the Mann-Whitney test, and the differences between species for both V1 and V2 were compared using the Mann-Whitney and Student’s t test respectively.

A multiple linear model was then constructed using the time required to return as the response (y-var) and distance plus time until stopping as the explanatory variable (x-var). Separate regression analyses for both predictors were conducted.

The times of day when the beetles left the nest were analyzed in order to discover possible patterns and peaks in *Corotoca* spp. trail visiting frequencies (leaving nest ~ time) by building a contingency table and using the χ^2 test. Correlation analysis among variables was conducted using Spearman’s rank. All of the analyses were conducted using R version 3.2.3 software (R Core Team, 2015).

RESULTS

Both species (*Corotoca melantho* and *C. fontesi*) display very similar reproductive behaviors in terms of larval extrusion (Table 1). The multiple linear models using Distance + Time until stopping as explanatory variables showed that both variables were significantly related to

Table 1. Descriptives of the sampled variables for each species during larvae extrusion, deposition, and returning to the nest of *Corotoca melantho* and *C. fontesi* along the foraging trails of its host (N = 24).

Descriptive	Species	Distance traveled	Time (seconds) until		V1	V2
			Stopping	Returning		
Mean	<i>C. fontesi</i>	24.0	30.5	64.0	1.48	4.06
	<i>C. melantho</i>	19.3	34.4	61.6	2.73	5.18
Median	<i>C. fontesi</i>	24.5	31.5	68.5	1.26	3.19
	<i>C. melantho</i>	17.5	22.0	61.0	1.43	3.18
SD	<i>C. fontesi</i>	14.4	16.6	26.9	0.878	2.98
	<i>C. melantho</i>	12.0	29.4	36.0	3.43	5.26

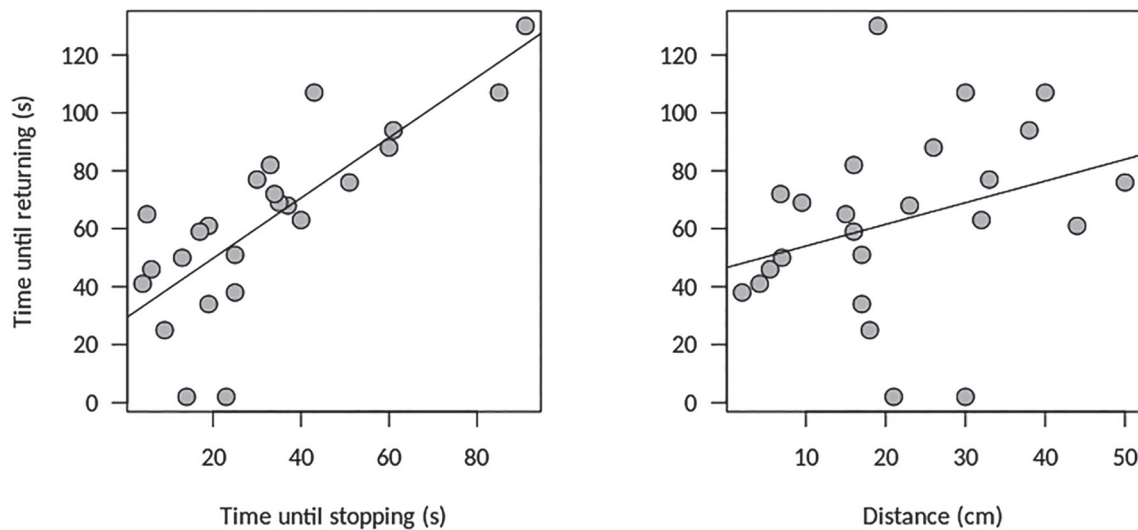


Figure 3. Simple regressions using each of the independent variables of the multiple linear regressions for time until extrusion and return to the nest by *Corotoca melantho* and *C. fontesi*. Left: return time (y-var) vs time until stopping (x-var) ($R^2 = 0.6152$; $F = 35.17$, $P < 0.001$); Right: return time vs distance traveled (x-var) ($R^2 = 0.10$; $F = 6.461$, $P = 0.13$).

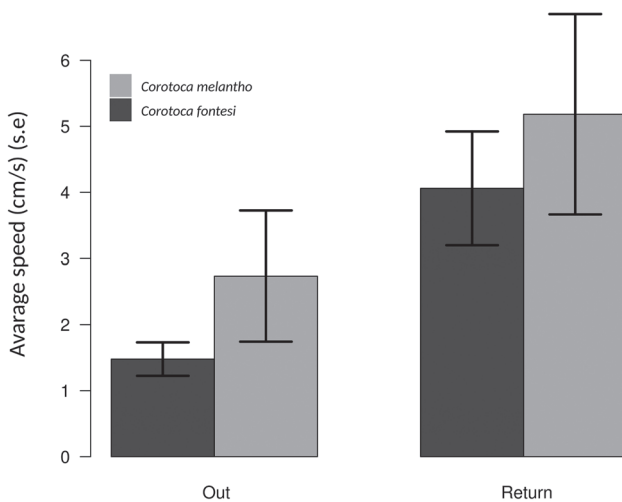


Figure 4. Bar plots of the average speeds of the two beetle species (bars represent the standard errors of the means). Lighter bars represent V1 (the out of nest velocity) while the darker bars represent V2 (the return speed). Higher speed spindle as are observed when returning to the nest.

the time until returning ($R^2 = 0.6203$; $P < 0.001$). The time until stopping ($F_{1,21} = 28.7478$; $P < 0.001$) and distance traveled ($F_{1,21} = 5.5645$, $P < 0.05$) both significantly influenced the response (return) (Fig. 3).

Surprisingly, the coefficient of Time to stopping (1.094) displayed a positive influence on the return time (31.477) while distance exhibited a negative effect (-0.193). That situation can be explained by the higher return speed (Fig. 4).

We observed statistical differences between the displacement speeds of the beetles and the direction that they were moving (both species) ($U = 137$; $P < 0.01$) (Fig. 3), with returning to the nest speeds (V2) being higher than those of leaving the nest (V1). There were no differences between the two species regarding V1 ($U = 62$; $P > 0.05$) and V2 ($T = -0.64307$, $d.f = 22$, $P > 0.05$) (Table 2), as both displayed a higher V2. We recorded 12 individuals of each species during the observations. The most beetles

Table 2. Pair-wise comparisons (by species) of the collected variables show no differences between *Corotoca melantho* and *C. fontesi* regarding larval deposition. A non-parametric test was used for non-normal variables (Time until stopping).

Variable	Test	Statistic	d.f	p
Distance (cm)	Student's T	0.867	22	0.395
Time until stopping(s)	Mann-Whitney's U	68	—	0.583
Return time(s)	Student's T	0.186	22	0.854

left the nest between 23 h and 01 h h (91.7, 66%). No significant statistical differences were observed in terms of the numbers of individuals leaving the nests at any sampling time ($\chi^2 = 12$, $d.f = 9$, $P > 0.05$).

DISCUSSION

We collected data on two species of viviparous Aleocharinae that live in exclusive relationships with their host. *Corotoca melantho* and *C. fontesi* displayed very similar behaviors of passive dispersal of their larvae, which raises the possibility that viviparity (as a character) and the behavior of dispersing immatures might represent a trait that evolved previous to the separation of *Corotoca* + *Spirachta* (sister groups), given that the latter species had also been observed accompanying the foraging parties of its host (*Constrictotermes cavifrons* Holmgren, 1910) (Kistner, 1969). Unfortunately, the viviparity of *Spirachta* is still to be confirmed (Zilberman et al., in prep).

We found that the distance traveled is not the main factor causing increased return time, but rather a higher average return speed (Fig. 4). Such behavior can be interpreted as a strategy to avoid predation, since termites are often attacked by natural enemies while foraging (Eisenmann, 1961; Sheppe, 1970).

Because the female is never found outside the nest without carrying at least a second larva, she not only risks

her own life, but the life of a future generation of individuals carrying her genes. The foraging trails of *C. cyphergaster* are guarded along their edges by a line of aggressive and quickly triggered soldiers, while workers move quickly in a single direction in the center (Moura et al., 2006) and the beetles are never seen along the margins of the termite trails (Oliveira et al., 2018). As pointed out by Hamilton (1971), when moving in groups, animals in the middle are safer than those along the edges. Therefore, walking among workers, and between lines of altruistic soldiers willing to sacrifice their own lives, can be interpreted as a strategy to increase the beetle's fitness. Traveling longer distances still presents a higher risk to the beetles (Magnhagen, 1991), however, although the farther away a mother leaves her brood, the less chance there is that the larva will return to the nest as a steno-gastric adult. We are still testing this hypothesis, but literature on the evolution of flightless beetles points to the fact that returning to the place of origin (nest) tends to diminish the genetic variability of the species and leads to greater genetic distances (Ikeda et al., 2012).

Regarding the fact that *Corotoca* spp. must stop in the middle of the foraging trail to deposit its larva, two principal hypotheses have been put forward: i) stopping is motivated by the physiological needs of the female rather than by any voluntary mechanism. Thus, the female would move forward on the trail until the moment of larval extrusion. This theory is actually corroborated by the positive correlation between those variables ($S = 1189.6$, $P < 0.05$); ii) the second hypothesis predicts that the mechanism of larval extrusion is fully (or largely) controlled by the female, and that the insect will walk in safety for as long as possible before extrusion. Therefore, as the larva reaches maturity within the maternal body, successful extrusion can occur wherever the mother beetle is. This theory is corroborated by the fact that when disturbed (in the laboratory), the females will usually expel a larva in a late stage of development, possibly as a strategy to save that offspring (as the larvae are much

more rapid and display more mobility than the adults) (Zilberman et al., in prep). Both theories might be wrong, or a combination of both might better fit the natural history of the genus.

Upon stopping, the female will recruit a worker to carry the larva (Oliveira et al., 2018). This does not happen immediately, however, and the beetles may employ some cue that signals "stop" to the termites, in a manner similar to that reported by Hölldobler (1971) and Quinet & Pasteels (1995) for myrmecophilous Aleocharinae. The existence of chemical signals is well recognized in the literature, and is extremely important to the organization of social insects (Czaczkes et al., 2015). As termites respond to the intensity of such cues, not all of the workers passing by the beetle would be expected to stop (given the marking by scout soldiers of cues that signal "follow the trail") as the "stop" signal of the female could be very faint.

As shown in Fig. 3 (Right), distance is not statistically influential in the return time response ($P > 0.05$) and is only weakly correlated to it ($R^2 = 0.10$) because individuals return much faster once larval extrusion occurs. The average speed of the returning beetles may increase because of the loss of the larval mass. When a nest was observed to have fallen from its support tree on one occasion, we observed *Corotoca* beetles following the termites into ground borrows (where a new nest would be constructed) at considerable speeds, which indicates that the beetles can move rapidly when necessary.

Our collection chart indicates that the beetles will come out of the nest within the short time span (three hours) of active foraging (Fig. 5). The beetles leave the nest solely to disperse their larvae, and that movement is completely dependent on the occurrence of foraging events; no beetles leave the nest before 23:00. The foraging of *C. cyphergaster* in the EESJC in the northeastern Caatinga region was observed to begin near 22:00 (Moura et al., 2006), but requires up to one hour to establish an intense flow (no data is available, however, for other sites). Given that environmental factors are oth-

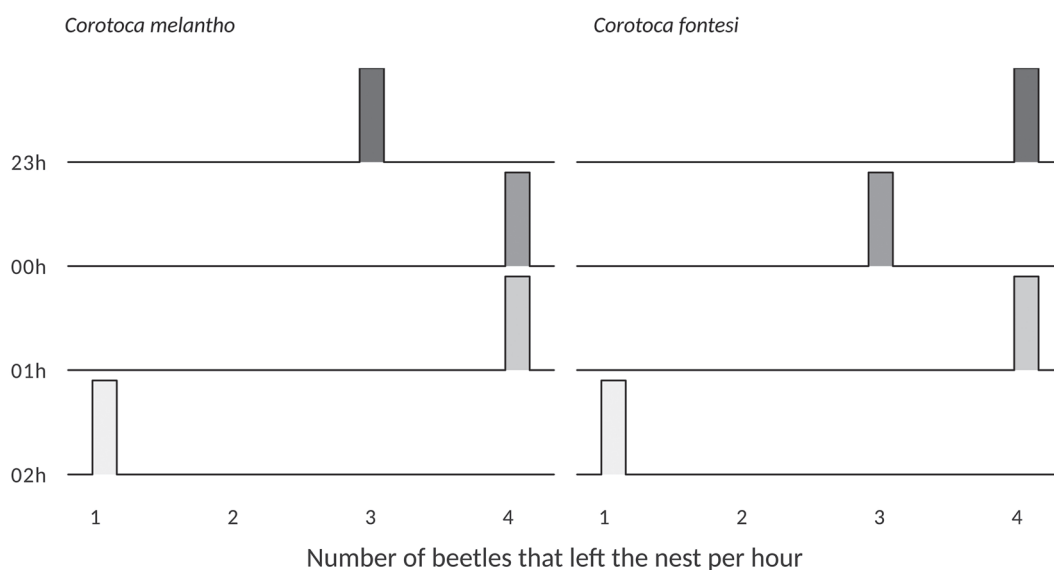


Figure 5. This model-chart represents the numbers of individuals leaving the nests each hour, by species (individuals leaving the nests during the 60 minutes that compose a given hour are grouped within the same hour).

erwise constant in the Caatinga domain, the trigger for *Corotoca* spp. exiting the nest is probably the intensity of termites in the foraging trail.

C. cyphergaster foraging occurs in "herds", but not all workers leave the nest simultaneously. Workers that have filled their crops will gradually return to the nest, and more workers will soon leave to feed (Bezerra-Gusmão, pers. obs.). This increased movement in the nest (between 22:00 and 23:00) can be interpreted by the beetle as a signal that foraging is occurring (although it will naturally decrease over time). As time passes, more workers tend to return to nest than leave it, which means that the chances of any worker carrying the larva upstream will decrease. The time at which this turnover of events occurs is approximately 02:00 (Moura et al., 2006), which agrees in detail with our sampling data (Fig. 5).

This paper is the second to describe the reproductive behavior of termitophile from field observations (following Oliveira et al., 2018), and reveals important points regarding termitophily and the life-cycle of viviparous Aleocharinae.

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