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Diurnal flight periodicity of a Neotropical ant assemblage (Hymenoptera, Formicidae) in the Atlantic Forest



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ABSTRACT

In this study we document for the first time flight patterns along a 24 h time range for an ant assemblage in one of the most diverse ecosystems on Earth, the Brazilian Atlantic Forest. Malaise traps were used to analyze the diurnal nuptial flights of a Neotropical ant assemblage during five days. Traps captured 802 individuals, revealing a remarkably high diversity (42 ant species), with samples strongly male biased (1:22). Contrariwise to similar studies, we found only a small proportion of species engaged in nocturnal nuptial flights, with diurnal flights accounting for an impressive 95% of all ant flight activity recorded. For the 18 most common species, three ant groups could be identified regarding flight period: sunrise, sunset, and continuous flight activity. Similarity analyses, however, suggest that closely related time ranges of flight activity may actually not be continuous. Further, three species showed pulsed flight activity, at varied hours of the day. Two species of *Hypoponera* showed flight activity at different periods of the day, suggesting congeneric staggered nuptial flights. Our results match long-term studies of ant assemblages showing high diversity of flight phenologies in hyperdiverse tropical ant assemblages and provide the first data on the reproductive phenology for several Neotropical ant species.

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Introduction

Despite the fact that ants are abundant and dominant members of almost every terrestrial ecosystem (Wilson and Hölldobler, 2005), surprisingly little is known about their reproductive ecology, apparently amounting to the works of Kaspari et al. (2001a,b), Dunn et al. (2007), Nascimento et al. (2011), Shik et al. (2012), and Helms and Kaspari (2014). Herein, we investigate the timing of reproduction, a key component of reproductive ecology. It influences the timing of subsequent life stages, the potential for hybridization, the forms of reproduction that are possible, and even potentially the ability of a species to coexist in local assemblages (Kaspari et al., 2001a; Dunn et al., 2007).

Due to its importance, reproductive behavior is precise and constant in most ant species (Andersen, 1991). With some exceptions, males and females have to rely on meeting each other for mating through nuptial flights (Noordijk et al., 2008). Ant colonies must synchronize flights so as to optimally outbreed, find a nest, and

begin the fledgling colony's growth phase (Kaspari et al., 2001b). In other words, nuptial flights reflect an ant colony's investment in sexual reproduction and dispersal. Yet, little is known about community-wide patterns of alates' phenology (e.g., see comments in Tschinkel (1991), and the short list of references in Nascimento et al. (2011)).

Most data on ant nuptial flights refer to species from temperate zones (Boomsma and Leusink, 1981; Dunn et al., 2007; Noordijk et al., 2008; Woyciechowski, 1987, 1992), and a considerable proportion of the information is based on the observation of a single flight or just a few swarm events (e.g., Eberhard, 1978; Conway, 1996; Buschinger, 2003). The few long-term studies available on the flight phenology of tropical ants deal predominantly with seasonal patterns (Kaspari et al., 2001a,b). The exception is the work of Torres et al. (2001), which presents the nocturnal periodicities of ant nuptial flights in the tropical island of Puerto Rico, using light traps inspected regularly throughout the year.

Precise information about the periodicity of ant nuptial flights through a 24 h time scale is largely unavailable, and limited to a few taxa (Kannowski, 1959, 1969; Hölldobler, 1976). Our aim was to describe the taxonomic and temporal patterns of nuptial flights of an ant assemblage in the tropics through a full 24 h time scale.

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Material and methods

This study was performed in the Boracéia Biological Station (BBS), a 96 ha area within a 16,450 ha watershed reserve of Atlantic rainforest, situated in the state of São Paulo, southeastern Brazil (23°38' S, 45°53' W). The BBS is inserted in the Tropical Atlantic morphoclimatic domain, 900 m above sea level. Descriptions of the local vegetation can be found in Wilms et al. (1996). The average annual rainfall between 1973 and 1994 was 2024 mm, and the mean temperature for the same period was 17.9 °C (DAEE, 1994).

Specimens were collected during five days with eight Malaise traps (Townes, 1972), with two groups of two traps distributed in each of the two main trails in the BBS (*Trilha dos Pilões* and *Trilha do Divisor*). In each group, the two traps were set at approximately 100 m one from another. The groups of two traps in each area were set at approximately 200 m from each other, and both groups of four traps were approximately at 1.5 km from each other. All traps were set along day 1 (21 February 2005), and then synchronously emptied at day 2, at 06:00 h (DST). Each trap was checked exclusively by one person. The traps were then checked every full hour, starting at 07:00 h of day 2. At every checking, the samples of each group of two traps were combined into one sample; this was done in order to generate more robust samples of 1 h intervals. A complete round of 24 h of sampling was achieved from the 06:00–07:00 h sample of day 2 to the 05:00–06:00 h sample of day 3, therefore generating 24 samples for each point (two Malaises), or 96 samples total (two points in each of the two trails). The process of hourly sampling was repeated another four times for the period comprehended between 06:00 and 18:00 h of days 3, 4, 5, and 6, for all traps, thus generating another 192 samples (48 samples/day × 4 days). The traps were not checked from 18:00 h in the evening to 06:00 h in the morning between days 4 and 7; the material collected during this period, for each night, was consolidated into a single sample for each Malaise trap pair, therefore generating 4 more samples each night, or 16 samples. Due to logistic problems, the 48 samples of one diurnal period (day 3) were pooled and the data excluded from the analyses, being used only as reference material for the identifications. Overall, 256 samples were used for the analyses.

All ant specimens were pinned and deposited in the *Museu de Zoologia da Universidade de São Paulo* (MZSP) ant collection. Material processing followed the procedures listed in Kaspari et al. (2001a,b). Ants were identified by the authors to species and morphospecies through the literature and by comparing the specimens with determined material at the MZSP. Females of all species were identified to genus, but our ability to identify alates to species varied across taxa. Keys are available for alates of only a few genera, and identified series in museums often lack associated alates. Males of ants are even more difficult to sort to species, because of their highly conservative morphology (Yoshimura and Fisher, 2011). They were then sorted to genus, when possible, and to species/morphospecies, in all cases relying heavily on matching specimens at the MZSP collection.

Ant flight activity at BBS was evaluated according to 13 time groups yielded by the experimental design: 12 diurnal 1 h periods (from 06:00–07:00 h to 17:00–18:00 h) and one period of nocturnal flights (18:00–06:00 h). Variation in daily flight activity was evaluated graphically, plotting the relationship between hour and number of individuals captured given subfamily, day, Malaise trap or the most frequent ant species. We describe these relationships fitting a nonparametric regression using a loess smoother (*loess* function in R; R Core Team, 2015). The diel flight activity of the local ant assemblage was further examined using cluster analysis based on unweighted arithmetic average as linkage method and Jaccard (binary) similarity measure, but results with Sorensen (quantitative) and Baroni-Urbani Buser (binary) coefficients produced identical tree topology. The

cluster analysis combined with Jackknife procedure to evaluate the stability of the dendrogram topology (Table 2) was performed at www2.biology.ualberta.ca/jbrzusto/cluster.php.

Results

Field work produced 256 useful samples, equivalent to 32 Malaise-trap days (original data available as supplementary material). A total of 802 individual alates from 42 ant species and 18 genera were collected. Malaise trap sampling was strongly male biased, with only 36 females captured, nearly 1:22. Alate catches per sample varied from just one individual (18:00–06:00 h) up to 139 individuals (14:00–15:00 h). Only 46 individuals (5.7%) were

Table 1

Abundance of alates captured at Reserva Biológica de Boracéia along 24 h of the day, during a period of 5 days.

Taxa	Males	Queens	Total alates
Amblyoponinae	15	–	15
<i>Stigmatomma armigerum</i> (Mayr, 1887)	13	–	13
<i>Stigmatomma elongatum</i> Santschi, 1912	2	–	2
Dorylinae	11	–	11
<i>Cerapachys</i> sp.	11	–	11
Ectatomminae	5	–	5
<i>Gnamptogenys</i> sp.	5	–	5
Formicinae	83	3	86
<i>Acropyga goeldii</i> Forel, 1893	83	3	86
Heteroponerinae	4	2	6
<i>Heteroponera dolo</i> (Roger, 1860)	–	2	2
<i>Heteroponera</i> sp.	4	–	4
Myrmicinae	290	10	300
<i>Acanthognathus rudis</i> Brown & Kempf, 1969	13	–	13
<i>Acanthognathus</i> sp.	23	–	23
<i>Crematogaster</i> sp.	2	–	2
<i>Hylomyrma reitteri</i> (Mayr, 1887)	85	1	86
<i>Octostruma rugifera</i> (Mayr, 1887)	16	–	16
<i>Pheidole</i> sp. 1	–	2	2
<i>Pheidole</i> sp. 2	–	1	1
<i>Pheidole</i> sp. 3	–	1	1
<i>Pheidole</i> sp. 4	22	–	22
<i>Pheidole</i> sp. 5	13	–	13
<i>Procryptocerus</i> sp.	1	–	1
<i>Rogeria</i> sp.	67	–	67
<i>Solenopsis</i> sp. 1	11	2	13
<i>Solenopsis</i> sp. 2	11	1	12
<i>Strumigenys saliens</i> Mayr, 1887	12	2	14
<i>Strumigenys</i> sp. 1	3	–	3
<i>Strumigenys</i> sp. 2	1	–	1
<i>Strumigenys</i> sp. 3	1	–	1
<i>Strumigenys</i> sp. 4	7	–	7
<i>Strumigenys</i> sp. 5	1	–	1
<i>Myrmicinae</i> sp.	1	–	1
Ponerinae	358	21	379
<i>Anochetus altisquamis</i> Mayr, 1887	1	–	1
<i>Hypoponera distinguenda</i> (Emery, 1890)	47	11	58
<i>Hypoponera iheringi</i> (Forel, 1908)	–	3	3
<i>Hypoponera trigona</i> (Mayr, 1887)	106	2	108
<i>Hypoponera</i> sp. 1	80	–	80
<i>Hypoponera</i> sp. 2	–	2	2
<i>Hypoponera</i> sp. 3	3	–	3
<i>Hypoponera</i> sp. 5	86	1	87
<i>Hypoponera</i> sp. 6	6	2	8
<i>Pachycondyla</i> sp. 1	16	–	16
<i>Pachycondyla</i> sp. 2	5	–	5
<i>Pachycondyla</i> sp. 3	3	–	3
<i>Pachycondyla</i> sp. 4	3	–	3
<i>Ponerinae</i> sp.	2	–	2
Total	766	36	802

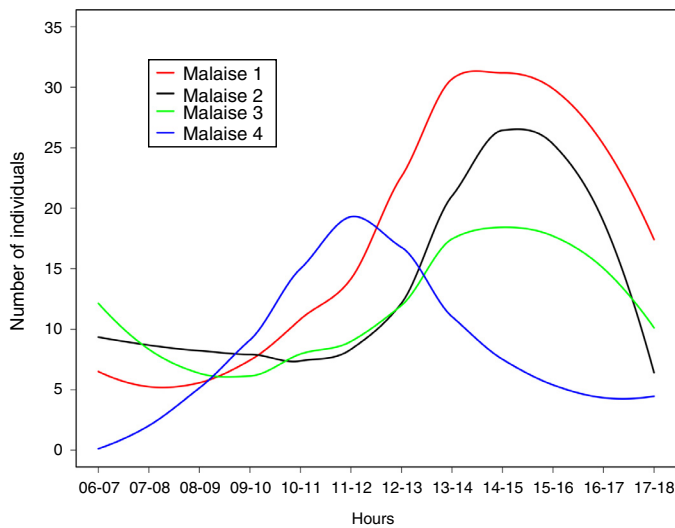


Fig. 1. The relationship between hour and flight activity of a Neotropical ant assemblage given sampling effort (four Malaise traps), based on hourly sampling summary from five days. The solid lines were obtained by the locally weighted smoother (function *loess* in R).

present in the nocturnal samples. Eight species were represented by a single individual and six by two individuals (Table 1).

Malaise traps sampled mainly the subfamilies Ponerinae and Myrmicinae, which accounted for 47.3% and 37.4% of the individuals, respectively. Formicinae comprised 10.7% of the catches. Similarly low values were found for Amblyoponinae (1.6%), Dorylinae (1.4%), Heteroponerinae (0.7%) and Ectatomminae (0.6%).

The monitored Malaise traps showed strong variation in the total number of daily flights (Fig. 1). Most individuals were recorded between 10:00 and 15:00 h. Both individual trap totals and the combined total number of individuals captured during the five days of observation (daily total) suggest that flight activity increases from dawn up to until 15:00 h, and then abruptly declines toward 18:00 h (Fig. 1). This is also somewhat evident on a day by day analysis (Fig. 2), and again for the Formicinae and Myrmicinae separately (Fig. 3). For other subfamilies, flight activity might appear to be continuous throughout the day, but there are too few specimens to allow for reliable conclusions (Fig. 3).

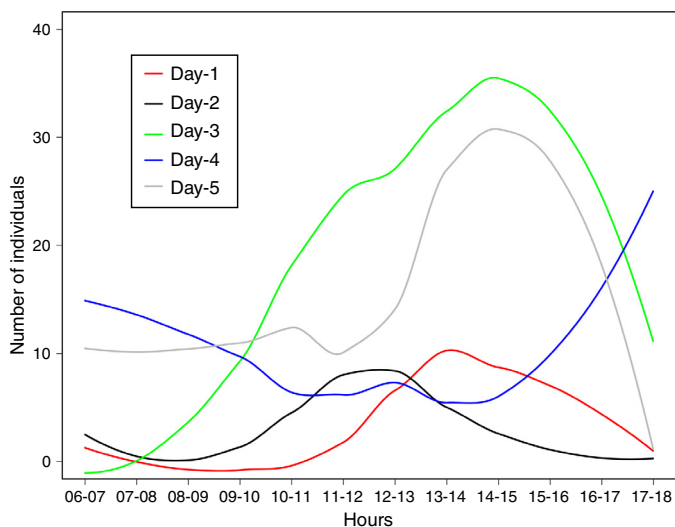


Fig. 2. The relationship between hour and flight activity of a Neotropical ant assemblage through a 24 h time scale. The solid lines were obtained by the locally weighted smoother (function *loess* in R).

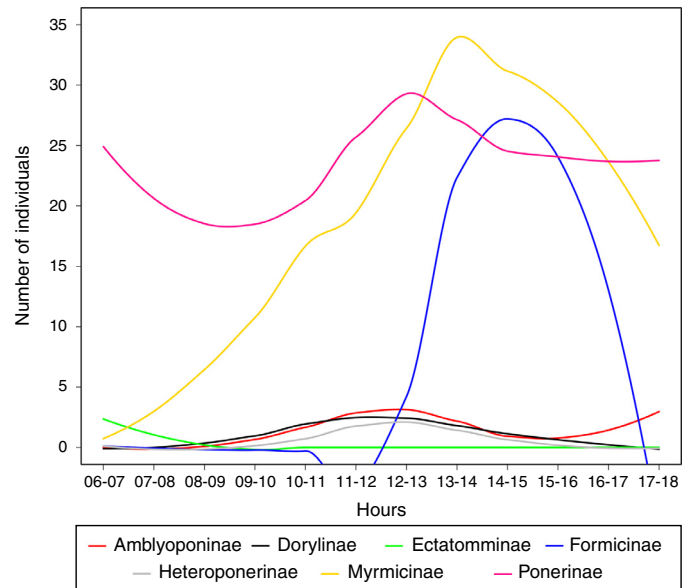


Fig. 3. The relationship between hour and flight activity of ant subfamilies from a Neotropical assemblage captured through a 24 h time scale. The solid lines were obtained by the locally weighted smoother (function *loess* in R).

Eighteen species with eight or more sampled individuals made up 92% of the combined trap catch (738 individuals). Flight activity hours along the 5 days varied much (Fig. 4a–c), occupying all time zones, in a distinct stratification pattern (Fig. 5). Visually, three quantitative clusters seem apparent in Fig. 5: three species in the 6–9 h range (top left), eleven species concentrating within 10–15 h, and then five species most frequently observed after 16 h. Similarity analyses (Table 2), on its turn, are quite consistent in suggesting three functional groups of flight activity: (1) 7–9 h and 16–18 h, (2) 9–12 h and 15–16 h, and (3) 12–15 h.

All *Hypoponera* species (Ponerinae) and *Hylomyrma reitteri* (Figs. 4a and 5), as well as, to a certain extent, *Rogeria* sp. (Myrmicinae) and *Cerapachys* sp. (Dorylinae) (Figs. 4c and 5) seem to fly continuously along the day, although *Hypoponera distinguenda* was more active in the first hours of the day (06:00–09:00 h). *Rogeria* sp. (Figs. 4c and 5) showed a wide range of diurnal flight activity, and a unimodal curve. In general, males of common species showed distinct and highly pulsed flight activity. *Acropyga goeldii* (Formicinae) and *Pheidole* sp. 1 (Myrmicinae) had a restrict period of flight with a strong pulse at 13:00–15:00 h (Fig. 4b), while *Pachycondyla* sp. 1 (Ponerinae) presented a strong pulse at 06:00–07:00 h (Fig. 4b). Trap-jaw species in the genera *Acanthognathus* and *Strumigenys* (Myrmicinae) seem to fly in the afternoon, between 14:00 and 18:00 h (Fig. 4c). Species known to possess thicker integument, *Pheidole* spp., *Solenopsis* spp., *Stigmatomma armigerum*, and *Octostruma rugifera*, flew at the hottest hours of the day. It is interesting that the two commonest species of *Hypoponera* have different nuptial flight peaks, with *H. distinguenda* flying early in the morning and *H. trigona* at sunset.

Discussion

Our data represent a first trial to describe in detail the flight phenology of a tropical ant assemblage. Daily and hourly sampling design for studying ant phenology is a complex and time-consuming task, stretched by the lack of taxonomic information regarding alate ants. Considering the relatively short exposition period of the Malaise traps, one notable finding of this study is the significant number of ant species collected (42 species in 18 genera). This fact is certainly related to the very high diversity of the

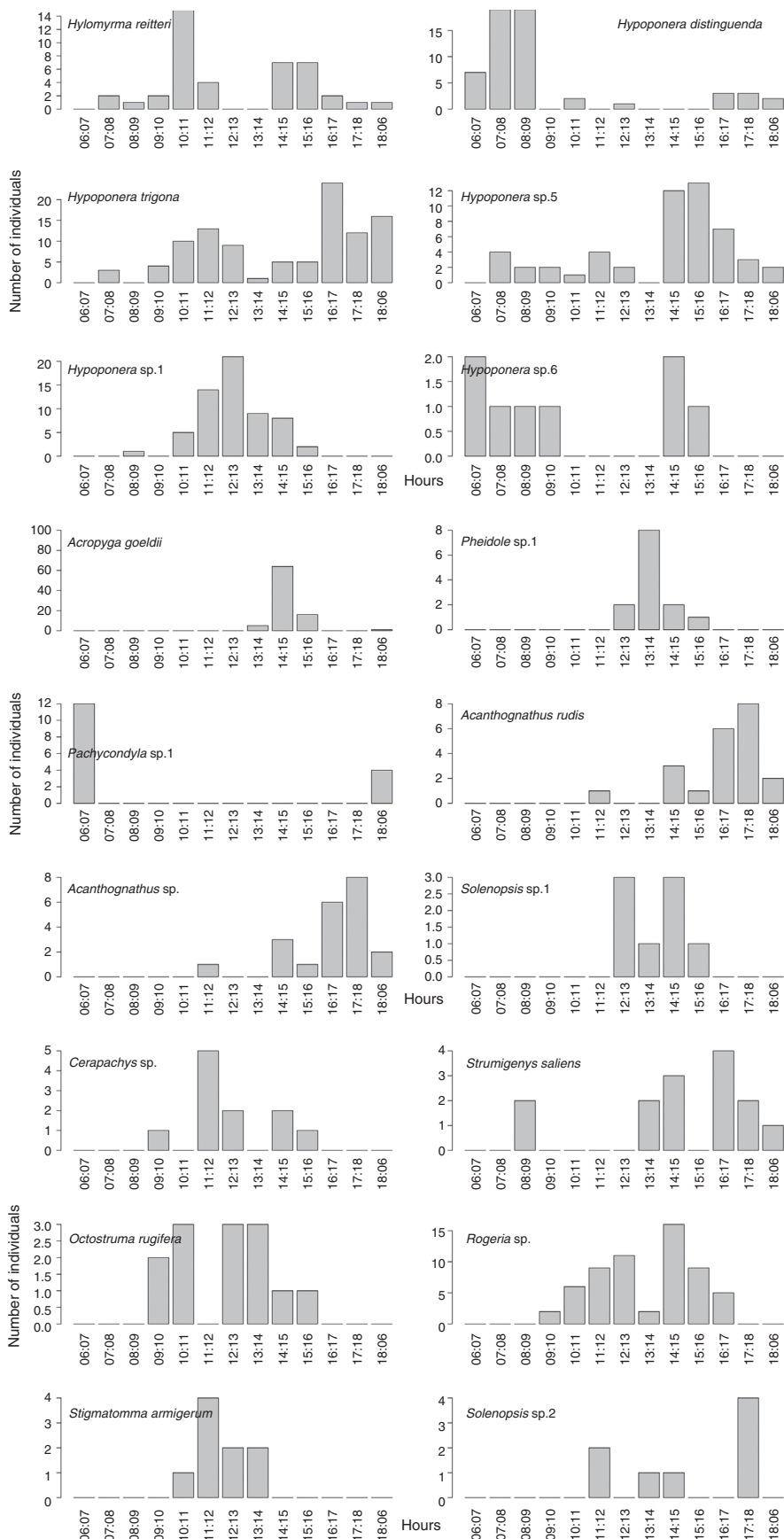


Fig. 4. Phenologies of flight activity of common species of a Neotropical ant assemblage in Atlantic Forest, southeastern of Brazil. Phenologies are the pooled activity from four Malaise traps and hourly sampling from five days.

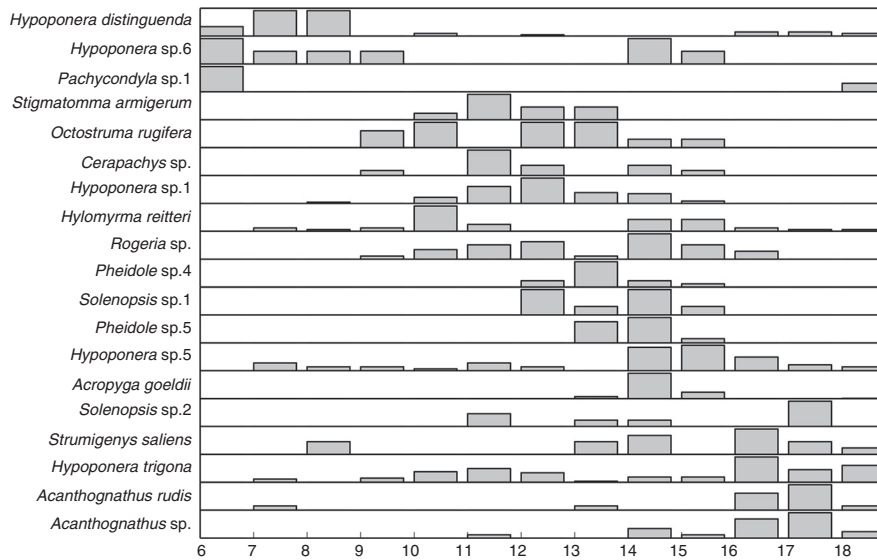


Fig. 5. Phenologies of flight activity for all species represented by eight or more specimens in total. Species are sorted on the vertical axis according to the pondered average of hour of flight, producing the observed diagonalization from early morning on top to nocturnal on the bottom. Frequencies are normalized from 0.0 to 1.0.

ant fauna in the Atlantic Forest biome (Silva and Brandão, 2010); further, Malaise traps may capture alate forms of the species living in different layers of litter and soil, as well as species restricted to vegetation (Castaño-Meneses et al., 2009). Indeed, Malaise trapping has been suggested as an efficient method to capture ants (in particular, the arboreal fauna) and in some applications could be a substitute for canopy fogging (Longino and Colwell, 1997).

Previous studies suggest that a considerable proportion of the ant species presents nocturnal nuptial flights (Kaspari et al., 2001a; Nascimento et al., 2004), and that this behavior could be a strategy to avoid diurnal predators and the risk of desiccation caused by high temperatures (Nascimento et al., 2011; Torres et al., 2001). Also, the crepuscular hours would be less windy than daylight hours, and therefore more favorable to the flight of small insects, as

Table 2
Clustering of time of flight activity based on all available data based on unweighted arithmetic average and Jaccard (binary) coefficient. Stability analysis: for each numbered node in the original tree, it is shown which percentage of 30 trees generated by Jackknife had an equivalent node. Two interior nodes (in different trees) are equivalent if they have the same samples as descendents.

Tree Topology	Distance	Stability analysis (%)	
+----06:00-07:00			
1 '	0.93444	100	
	+----07:00-08:00		
	5 '	0.50000	97
	+----08:00-09:00		
	3 '	0.62194	100
	+----16:00-17:00		
	6 '	0.25000	100
	+----17:00-18:00		
+----2 '	0.76071	100	
	+----09:00-10:00		
	11 '	0.44444	87
	+----10:00-11:00		
	9 '	0.51894	97
	+----11:00-12:00		
	7 '	0.66190	67
	+----15:00-16:00		
+----4 '	0.67394	97	
	+----12:00-13:00		
	8 '	0.58493	93
	+----13:00-14:00		
	10 '	0.50000	100
	+----14:00-15:00		

ants (Baldridge et al., 1980). Contrariwise, this study found that a small proportion of species had nuptial flights during the night, and that diurnal flights account for an impressive 95% of the ant flight activity. In the Atlantic Forest of southeastern Brazil, the variation of temperature, moisture, and wind speed between diurnal and nocturnal periods is less pronounced than in open and/or drier tropical biomes (Vieira et al., 2015), which could help to explain the high number of diurnal flights.

It has also been suggested that nocturnal predators such as bats, frogs, nocturnal wasps, and others, can also cause significant losses during ant nuptial flights (Levin et al., 2009). This could be somehow related to the scarce catchings in nocturnal samples, but also represents a selective pressure that speaks in favor of diurnal flights. In addition, our results suggest that species with thickest integument (i.e., Dorylinae, Myrmicinae, and Ponerinae ants in this study) may extend the flight period for several hours along the day, including the hottest periods, which might possibly be related to a higher ability to reduce water loss. Torres et al. (2001) also found that queens start to fly earlier in the day than males, and that could explain the low number of males in the pre-dawn period (04:00 to 06:00 h).

Malaise traps were extraordinarily male biased in this study, and this is consistent with other neotropical ant assemblage surveys (e.g., Kaspari et al., 2001a,b) and taxonomic studies (e.g., Yoshimura and Fisher, 2012). Our sampling design with data on flights at specific times of the day also provided strong evidence of a high diversity in phenology for ant species in the Atlantic Forest, even though most species presented highly asynchronous interspecific flights. Nuptial flight synchronization has been associated with predator avoidance, maintenance of reproductive isolation and outbreeding promotion (Torres et al., 2001).

As described in other studies on the neotropical ant fauna, flights of Dorylinae, Formicinae, Myrmicinae, and Ponerinae may occur at equal times of the day (Kaspari et al., 2001a; Torres et al., 2001). Species of other typical Neotropical ant subfamilies as Dolichoderinae, Proceratiinae or Pseudomyrmecinae were absent in our Malaise samples, but this may not be straightforwardly related to sampling efforts. Dolichoderinae, for example, includes species in which nuptial flights contain few individuals (Torres et al., 2001). In addition, leaf-litter sampling at BBS suggests that Dolichoderinae species are not common in Atlantic Forest (Silva and Brandão, 2010).

This study is the first to investigate flight patterns along a 24 h time range for an ant assemblage in the tropics, and despite representing only a 5-day snapshot, relevant findings emerged. A high species richness was found at the study site, and males of the sampled subfamilies probably prefer to have nuptial flights during the day. Flight activity of ant males at BBS fall into three groups: sunrise, sunset, and flights during most of the day. Similarity analyses, however, suggest that closely related time ranges of flight activity may actually not be continuous (Table 2). This might make sense, since climatic fluctuations along daytime are approximately bimodal (morning/afternoon). This is further supported by the aggregations of males of different species of the most frequent ant genus in this study, *Hypoponera*, observed at different periods of the day, suggesting staggered flights of congeneric species within the narrow range of a single hour of the day.

Finally, some species seem to show a clearly pulsed flight activity, happening at different periods of the day. Overall, this study reveals a rich, perhaps even surprising, diversity of flight phenologies for Atlantic Forest ants.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.rbe.2016.05.006.

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