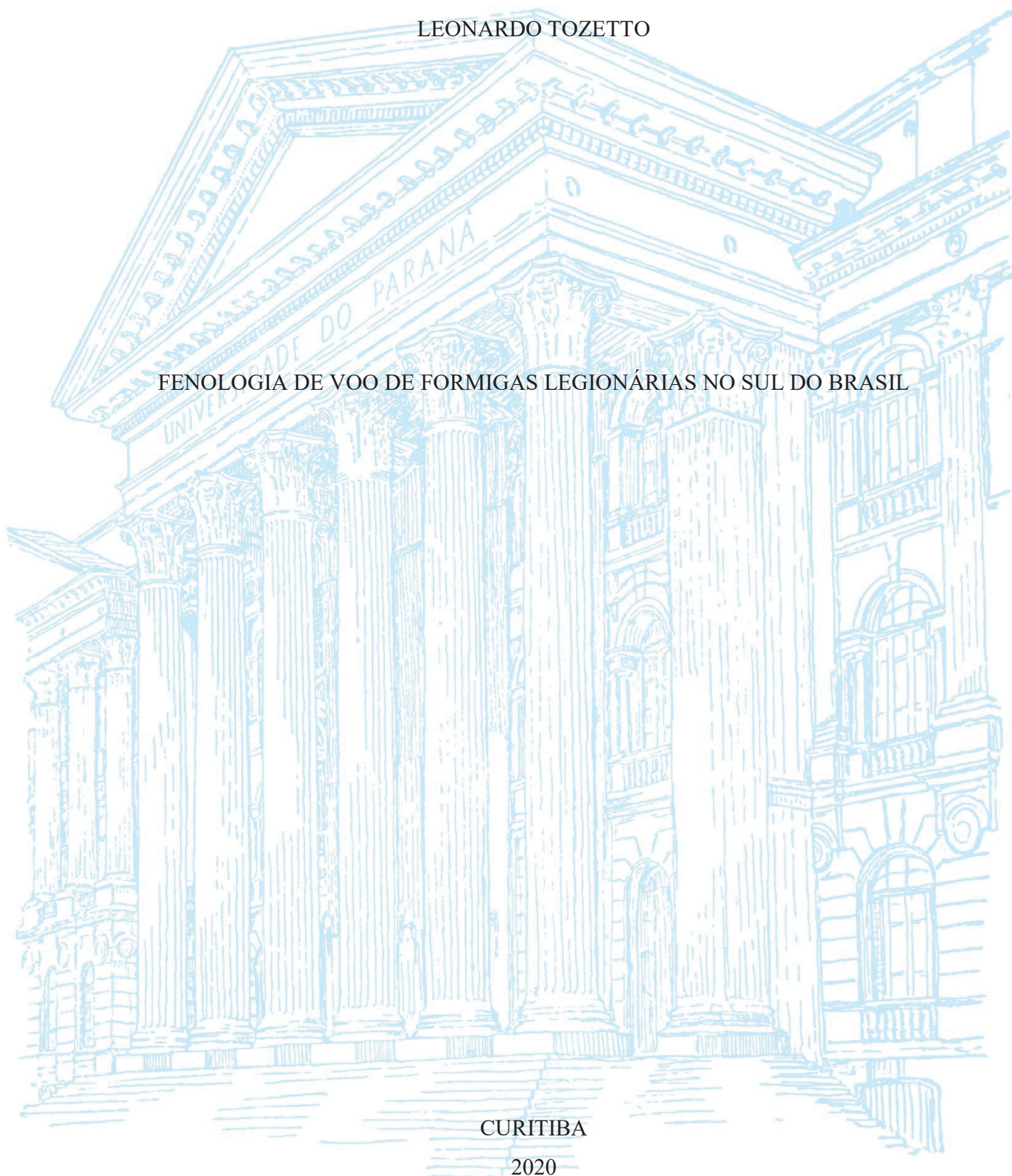


UNIVERSIDADE FEDERAL DO PARANÁ

LEONARDO TOZETTO

FENOLOGIA DE VOO DE FORMIGAS LEGIONÁRIAS NO SUL DO BRASIL



CURITIBA

2020

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FENOLOGIA DE VOO DE FORMIGAS LEGIONÁRIAS NO SUL DO BRASIL

Dissertação apresentada ao curso de Pós-Graduação em Ciências Biológicas (Entomologia), Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Mestre em Ciências Biológicas (Entomologia).

Orientador: Prof. Dr. John E. Lattke

Coorientador: Prof. Dr. Sebastian Sendoya

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em CIÊNCIAS BIOLÓGICAS (ENTOMOLOGIA) da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **LEONARDO TOZETTO** intitulada: **Fenologia de voo de formigas legionárias no sul do Brasil**, sob orientação do Prof. Dr. JOHN EDWIN LATTKE BRAVO, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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Como tem corrido esse tempo. Há de ter voado, fugido, evaporado – não se pode dizer como. Eram, afinal de contas 24 meses em que eu deveria passar em companhia da dissertação, um longo tempo, cujo fim, no início, parecia muito distante. E agora, de repente, não sobravam mais do que poucas semanas, um resto insignificante, que, na verdade, se tornava um pouco mais importante pelas variantes periódicas do programa habitual, mas sobre o qual já pesava o pressentimento da arrumação das malas e da despedida. Vinte e quatro meses não representam quase nada. Todos haviam me prevenido desse fato. Talvez fosse devido ao aumento da combustão cerebral que o tempo corria ali tão vertiginosamente. Mas durante esses vinte e quatro meses deveria ter prestado maior atenção ao curso dos dias. Sinto sincera paixão por esse lapso de tempo. Uma compaixão tão ardente que em certos momentos me dói o coração, e tão viva que as vezes me pergunto seriamente a mim mesmo se tenho coragem de deixá-lo. É verdade que as memórias construídas foram muito vastas, as impressões recebidas, as conversas trocadas – lhes devo ao grande número de ideias. Não me parece que já digeri tudo isso ou que me aclimatei. Não, não se pode falar, no meu caso, de aclimação. E nem é possível com tão pouco tempo. Seria preciso uma permanência mais longa para a gente se adaptar e assimilar as impressões novas. É uma lástima. Devo muito aos que me fizeram companhia durante minha estadia. Às boas vindas do Rodrigo e do laboratório. Depois da primeira visita, da primeira impressão, não foi possível ir embora. Ao John, pela confiança e otimismo, pela companhia e pelos cafés.

RESUMO

As formigas legionárias são uma das mais impressionantes formas de vida encontradas na região Neotropical. Elas são caracterizadas por grandes colônias nômades e pela predação em grupo. Neste grupo, as fêmeas nunca desenvolvem asas, sendo que apenas os machos são alados e representam o único agente de dispersão, tendo uma importância fundamental na manutenção da diversidade genética. Aqui avaliamos a fenologia do voo nupcial de formigas legionárias, amostradas continuamente ao longo de dois anos por meio de armadilhas de luz dispostas em oito localidades do estado do Paraná, Brasil. Testamos a temperatura e a umidade como preditoras para a abundância dos machos considerando o período que antecede o voo e nos dias do voo. No total, 6330 machos foram coletados, pertencentes a 22 espécies dos gêneros *Eciton* (3 espécies), *Labidus* (3 espécies), *Neivamyrmex* (14 espécies) e *Nomamyrmex* (2 espécies). As espécies de *Neivamyrmex* e *Nomamyrmex* possuem um período reprodutivo mais restrito aos meses mais quentes; *Eciton* e *Labidus* apresentam período reprodutivo mais amplo, além de uma maior segregação entre o voo das espécies. Nossos resultados também mostram um efeito importante da temperatura no dia do voo, e uma resposta mais variável quanto à umidade.

Palavras-chave: Dorylinae. Reprodução. Voo de acasalamento.

ABSTRACT

The army ants are one of the most remarkable life forms found in the Neotropical region. They are characterized by an unusual combination of behavioral traits and are among the top arthropod predators in the tropical ecosystems. Nevertheless, knowledge of their biology is limited to some model species. For most species, their biology is unknown as many are subterranean and their population tend to show low abundances. In this group, gynes are permanently wingless, so winged males represent the only dispersal agent and have key importance in maintaining genetic diversity. Males can tell us many things, such as the presence and diversity of rarely collected species and much about their reproductive biology. Here we evaluate the mating flight phenology of army ants sampled continuously over two years from light traps placed in eight localities throughout the state of Paraná, Brazil. We test the influence of temperature and humidity in the pre-flight period and in the day-of-flight period on the abundance of males. We recorded 6330 males, belonging to 22 species: *Eciton* (3 species), *Labidus* (3 species), *Neivamyrmex* (14 species) and *Nomamyrmex* (2 species). *Neivamyrmex* and *Nomamyrmex* have species with a more restricted flight season, usually around October to March. While *Eciton* and *Labidus* have species with wider flight seasons and higher segregation among the species of the genus. Our results report a common positive effect of day-of-flight temperature among the species, but a more variable response to pre-flight or day-of-flight humidity.

Key-words: Dorylinae. Mating flights. Reproduction.

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1 INTRODUÇÃO

As formigas abdicaram de suas asas para realizar atividades diárias, como forragear, construir o ninho e cuidar da prole. No entanto, a colônia depende dos alados para a reprodução. Na maioria das espécies de formigas, colônias maduras investem anualmente grande quantidade de energia na produção de machos e fêmeas aladas que, durante o período reprodutivo, voam para copular com indivíduos de outras colônias (Hölldobler & Wilson, 1990). Após a cópula, as fêmeas procuram por locais adequados para fundar uma nova colônia e então perdem suas asas. No entanto, em muitos gêneros pode ocorrer a ausência do voo entre a casta reprodutora, geralmente mais comum entre as fêmeas. (Peeters, 2012).

A produção e liberação de alados pode acontecer em diferentes períodos do ano e horas do dia, o que confere diferentes padrões fenológicos (Kaspari *et al.*, 2001a; Feitosa *et al.*, 2016). A fenologia do voo é moldada por uma série de fatores bióticos, abióticos e endógenos, além de dizer muito sobre estratégias reprodutivas, seleção de habitats e estrutura de acasalamento (Talbot, 1965; Keller & Genoud, 1997; Corlet, 1988; Frederickson, 2006). A época da reprodução pode influenciar o sucesso reprodutivo dos organismos e reflete adaptações a diversos ambientes e estratégias de vida (Rathcke & Lacey, 1985; Kaspari *et al.*, 2001a).

Temperatura e pluviosidade geralmente são considerados chaves para compreender os padrões de fenologias encontrados em formigas (Kaspari *et al.*, 2001a; Dunn *et al.*, 2007; Noordijk *et al.*, 2008; Staab & Kleineidam, 2014). Esses fatores podem ter um papel regulador do ciclo reprodutivo tanto em uma escala anual, relacionado à época de aparecimento dos alados na colônia (Boomsma & Leusink, 1981; Kipyatkov & Lopatina, 1993), quanto em uma escala mais pontual, atuando no período da pré-revoada, ou responsáveis pelo disparo dos voos (Boomsma & Leusink, 1981; Torres *et al.*, 2001).

Todavia, os fatores precisos que desencadeiam a revoada são desconhecidos para a maioria dos grupos de formigas, principalmente devido às dificuldades de observação, como, por exemplo, o horário exato dos voos e a identificação dos alados, em especial os machos. Outro fator complicador é como diferentes fatores ambientais podem se combinar para determinar a produção de alados e sua liberação. Possivelmente há também uma relação entre o modo de fundação da colônia e uma maior ou menor dependência dos fatores climáticos envolvidos no momento dos voos (Passera e Keller, 1989). Por exemplo, colônias que se reproduzem por fissão, parecem ser menos dependentes dos fatores climáticos no disparo dos voos, e podem ser capazes de se reproduzir durante grande parte do ano (Kaspari *et al.*, 2001ab; Torres *et al.*, 2001)

As formigas legionárias são distintas de outras formigas por terem grandes colônias nômades que performam ataques em grupo e se dividem por fissão (Gotwald, 1995). Essas formigas fazem parte do grupo *Eciton* de gêneros: *Cheliomyrmex* Mayr, *Eciton* Latreille, *Labidus* Jurine, *Neivamyrmex* Borgmeier, e *Nomamyrmex* Borgmeier (Borowiec, 2016). Consideradas como predadoras topo de cadeia na serapilheira e no solo (Schneirla, 1971; Powell, 2011; Kaspari *et al.*, 2011; Hoenle *et al.*, 2018), estima-se que cada metro quadrado de uma floresta tropical é diariamente visitado por, pelo menos, uma espécie de formiga legionária (Quiroz Robledo *et al.*, 2002; O'Donnell *et al.*, 2007). Além do seu impacto como predadores, a importância ecológica dessas formigas é também relacionada à quantidade considerável de associações com diversas outras espécies de animais, tanto invertebrados quanto vertebrados. Por exemplo, Rettenmeyer *et al.*, (2011) registraram mais de 600 espécies associadas a *Eciton burchellii* e muitas dessas espécies são dependentes dessas formigas para sobreviver.

A maior parte das espécies é adaptada à vida subterrânea e são raramente encontradas na serapilheira, sendo denominadas hipogéicas. Por outro lado, o predomínio dos estudos se concentra nas poucas espécies que são comumente encontradas forrageando e estabelecendo *bivouac* na serapilheira, as epigéicas (Rettenmeyer, 1963; Gotwald, 1995; Kaspari e O'Donnell, 2003; Berghoff *et al.*, 2008). Embora hipogéica e epigéica sejam termos úteis, precisam ser aplicados com cuidado quando envolvem as formigas legionárias porque uma mesma espécie pode ter diferenças no uso do estrato de forrageamento, no local de migração e de estabelecimento do *bivouac*. Por exemplo, algumas espécies possuem *bivouacs* hipogéicos mas são forrageadoras epigéicas (Gotwald, 1995).

Em relação a casta reprodutora das formigas legionárias, as rainhas se destacam por serem as mais atípicas rainhas de todas as espécies de formigas, sendo referidas como rainhas dictadiformes devido a sua morfologia peculiar (Gotwald, 1995). Elas são cegas ou possuem olhos reduzidos ou vestigiais, não possuem asas, e são muito maiores que as operárias, possuindo o gáster desmedidamente expandido (Borgmeier, 1955). Os machos são robustos e bastante maiores que as operárias, assemelhando-se as rainhas, por outro lado, possuem grandes olhos compostos e mandíbulas bastante desenvolvidas (Borgmeier, 1955). Os machos são alados, e devem voar em busca de uma nova colônia para copular com uma jovem rainha. Por essa razão eles possuem uma importância chave na dispersão e fluxo gênico nas formigas legionárias. Sendo frequentemente coletados em armadilhas luminosas (Borgmeier, 1955; Nascimento *et al.*, 2011).

Poucos estudos exploraram as estratégias reprodutivas e a fenologia do voo dessas formigas na América do Sul (Nascimento *et al.*, 2004; Nascimento *et al.*, 2011). O manuscrito

a seguir aborda a fenologia de voo de formigas legionárias em uma escala regional no estado do Paraná. Além de explorar fatores climáticos relacionados com o desenvolvimento dos machos na colônia e com o disparo dos voos.

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3 INTRODUCTION

Ants gave up their wings for a life on the ground, where they perform daily tasks such as foraging, feeding the brood, and building the nest, all with a wingless worker caste. Yet the reproductive caste still mostly relies on flying to mate and found new colonies (Hölldobler & Wilson, 1990). In most ant species, males and reproductive females fly to mate with individuals from other colonies, and afterwards, the females look for nesting sites to establish their colonies. In some cases, the absence of flight does occur in the reproductive caste, mostly among females, pattern that has independently evolved in more than 50 genera (Peeters, 2012). However, even in these cases, generally one flying individual remains to disperse. The flight period is the deadliest phase in the ant life cycle, as they are exposed to predation and adverse environmental conditions (Peeters & Ito, 2001; Bonte *et al.*, 2012).

Most ant colonies allocate resources to reproduction on an annual schedule. The occurrence of the flight in different periods of the year or hours of the day results in different phenological patterns and reproductive strategies (Keller & Genoud, 1997). Ant species may vary in the duration of their mating flights. The flights may be as short as few hours on a single day (Talbot, 1968; Hölldobler & Wilson, 1990) or so long that they are nearly continuous throughout the year (*e.g.* Kaspari *et al.*, 2001a). The time and duration of reproduction and flight phenology are shaped by a variety of biotic and abiotic factors (Corlett, 1988). Moreover, this phenology of reproduction and dispersal in ants must simultaneously satisfy the timing of flights to optimally outbreed, found a nest, and favor the new colony's early growth (Andersen, 1991; Kaspari *et al.*, 2011a). Such mass emergences may also constitute a brief period of prey abundance, making ants likely to be important in aerial trophic interactions within ecosystems (Levin *et al.*, 2009).

Temperate regions have seasonal cycles that are usually predictable, with a determined amount of heat and light during a few weeks or months of the year. This is paralleled by the flights of temperate ants that usually have these events once in a year, in short periods that are highly synchronized (Boomsma & Leusink, 1981; Dunn, *et al.*, 2007). On the other hand, tropical regions provide a year-round window of opportunity for flying and nest founding (Kaspari *et al.*, 2001b). Flights in tropical regions must then be balanced between synchronous when good conditions for one species are also good for other related species, and asynchronous when related species give greater weight to promoting reproductive isolation (Kaspari *et al.*, 2001a). In tropical areas, where the temperature is more constant throughout the year, rain seems to play a more important role in flight synchronization among the colonies. It minimizes

dehydration of the winged individuals and facilitates nest excavation for the foundresses (Staab & Kleineidam, 2014). Climatic factors may play an important role in the reproductive cycle on an annual scale in relation to the development of winged ants in the colony (Boomsma & Leusink, 1981; Kipyatkov & Lopatina, 1993), as well as on a shorter time scale, during the pre-flight period, or on the trigger of flights (Boomsma & Leusink, 1981; Torres *et al.*, 2001).

Because many organisms respond to climate, shifts toward phenologies have been increasingly noticeable signs of climate change and thus an important component of the study in ecosystems (Thackeray *et al.*, 2010; Ellwood *et al.*, 2011; Forrest, 2016). Despite its importance, our knowledge of tropical ant flight phenology and of the environmental cues that trigger them remains incomplete, in part because current research in flight phenology is often highly localized spatially or temporally (Kaspari *et al.*, 2001ab; Nascimento *et al.*, 2004; Nascimento *et al.*, 2011; Feitosa *et al.*, 2016). Further progress on understanding the role of weather in tropical areas will only be possible with data covering a wider geographical area and a longer time period than as in previous studies.

Doryline ants are a monophyletic group that includes the true army ants, which represents approximately 156 species from the *Eciton* genus-group: *Cheliomyrmex* Mayr 1870, *Eciton* Latreille 1804, *Labidus* Jurine 1807, *Neivamyrmex* Borgmeier 1940, and *Nomamyrmex* Borgmeier 1936 (Borowiec, 2016). They are distinct from other ants by having large nomadic colonies that perform mass raids and divide by fission (the “army ant adaptive syndrome”, Gotwald, 1995). Their great impact on the diversity of leaf litter and soil arthropods is related to their role as top arthropod predators, making them keystone species in tropical ecosystems (Schneirla, 1971; Powell, 2011; Kaspari *et al.*, 2011; Hoenle *et al.*, 2019). Also noteworthy is their relationship with a considerable amount of animal species, both vertebrate and invertebrate. One study registered over 600 species of associated organisms for *Eciton burchellii* alone (Rettenmeyer *et al.*, 2011), many of which are totally dependent on these ants for their survival. Despite being important for ecosystem functioning, the basic biology and ecology of most army ant species remain poorly studied (Gotwald, 1995; Kronauer, 2009). For instance, few studies have explored army ant reproductive strategies and flight phenology in South America (Nascimento *et al.*, 2004; Nascimento *et al.*, 2011). Because reproductive females are flightless and never leave their colony, males must fly between colonies and run the gauntlet of the workers to get the young queen. For this reason, males have key importance in dispersal and maintaining genetic diversity in army ants. Being particularly easy to collect with light traps and with a relatively good taxonomy that encompasses males, army ants are a valuable group for exploring reproductive strategies.

The aim of the present study was to address some of these gaps in our knowledge about army ant regional diversity and investigate their mating flight phenology diversity during two years in a regional context of southern Atlantic forest of the state of Paraná, Brazil. Specifically, we addressed the following questions: (1) Does the abundance and richness of army ants fluctuate over time? (2) Is the flight of different army ant species synchronized? (3) Are there temperature and humidity drivers for flight phenology in this group? (4) Are these factors more related to pre-flight periods or during the flight?

4 MATERIAL AND METHODS

4.1 STUDY AREA

Data in this study were obtained from the *Levantamento da Fauna Entomológica no Estado do Paraná* project (PROFAUPAR). The state of Paraná includes five large geographic divisions: the eastern coast, escarpments of the crystalline complex, and the first, second and third plateaus in westward succession (Maack, 1981). Aiming to sample areas representing the aforementioned environments, the PROFAUPAR project sampled insects in eight localities of these five geographical divisions. **(1)** Antonina, Sapitanduva (25°28'S, 48°50'W), with an altitude of 60 m and an Af Köppen climate (Kottek *et al.*, 2006); **(2)** São José dos Pinhais, Serra do Mar (25°34'S, 49°01'W), with altitude 1050 m, Cfb climate; **(3)** Colombo (25°20'S, 49°14'W) with altitude 914 m, Cfb climate; **(4)** Ponta Grossa, Parque Estadual de Vila Velha (25°14'S, 50°03'W), with altitude 880 m, Cfb climate; **(5)** Jundiá do Sul, Fazenda Monte Verde (23°26'S, 50°16'W) with altitude 500 m, Cfa climate; **(6)** Telêmaco Borba, Reserva Biológica Klabin (24°17'S, 50°37'W), with altitude 750 m, Cfa climate; **(7)** Guarapuava, Santa Clara (25°40'S, 52°01'W), with altitude 740 m, Cfb climate; **(8)** Fênix, Reserva de Vila Rica (23°54'S, 51°58'W), with altitude 350 m, Cfa climate. According to the Köppen classification, the region is marked by a warm temperate, fully humid with well-distributed precipitation along all the year and ranging between hot summers and warm summers (Kottek *et al.*, 2006). Detailed descriptions of each locality can be found in Marinoni & Dutra (1991).

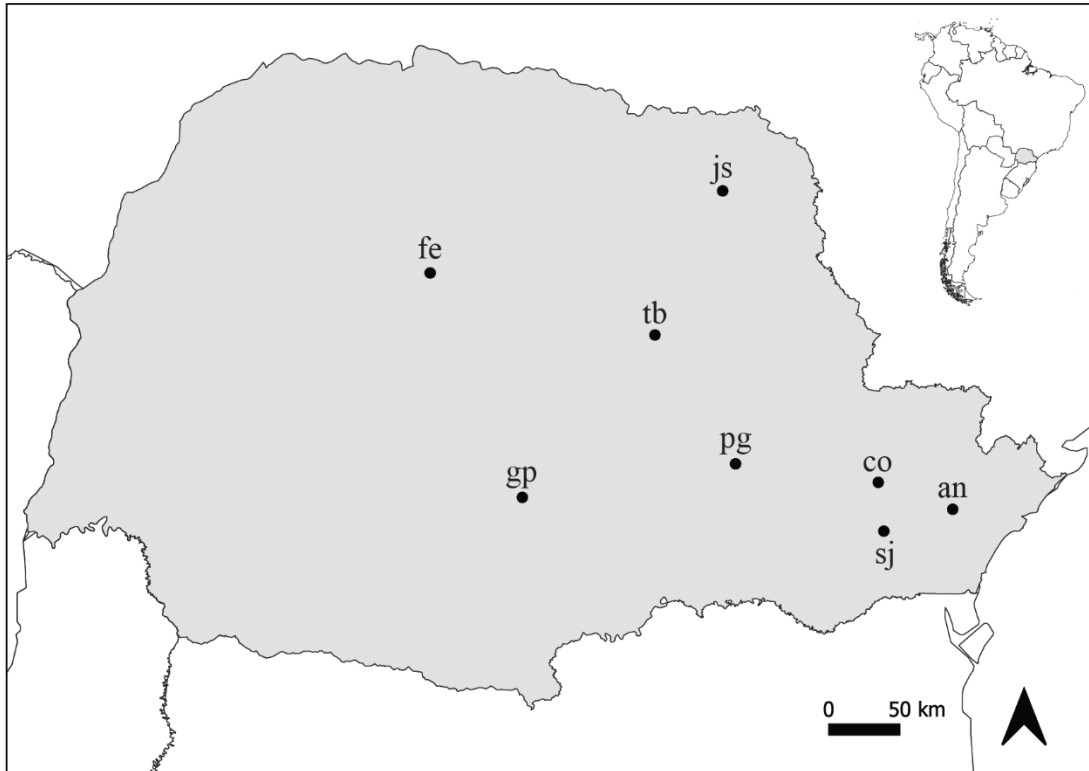


Figura 1 – Location of PROFAUPAR sampling sites in Paraná State . **an**: Antonina, **co**: Colombo, **fe**: Fênix, **gp**: Guarapuava, **js**: Jundiá do Sul, **pg**: Ponta Grossa, **sj**: São José dos Pinhais, **tb**: Telêmaco Borba.

4.2 SAMPLING AND SPECIES IDENTIFICATION

Army ant males were sampled with an *ESALQ* type light trap (Silveira Neto & Silveira, 1969) with a 160W mixed mercury vapor lamp modified by Marinoni & Dutra (1991). The light traps were kept running from 19:00 to 07:00, alternating from one hour on and then one hour off. Traps were kept running for five consecutive days during each lunar period, with the median day being the novilunium (new moon). They were emptied daily. The light traps were set up from August 1986 to July 1988 taking in a total of 25 new moons. In Antonina, sampling started in October 1986.

The ants were preserved in 70% ethanol and mounted and labeled for identification. Identification was carried out using taxonomic keys, descriptions, and illustrations provided by Borgmeier (1955). In addition to external morphological analysis, we dissected some individuals of each species to observe the genitalia. The dissections were carried out in 70% ethanol using fine forceps. Specimens from the PROFAUPAR Project are deposited in the Padre Jesus Santiago Moure Collection, Departamento de Zoologia, Universidade Federal do Paraná (UFPR), Brazil.

Temperature and relative humidity were recorded daily in each sampling area (Marinoni & Dutra, 1991). For São José dos Pinhais temperature data was not available at the time, henceforth we use climatic data from Colombo, a site 35 km from São José dos Pinhais.

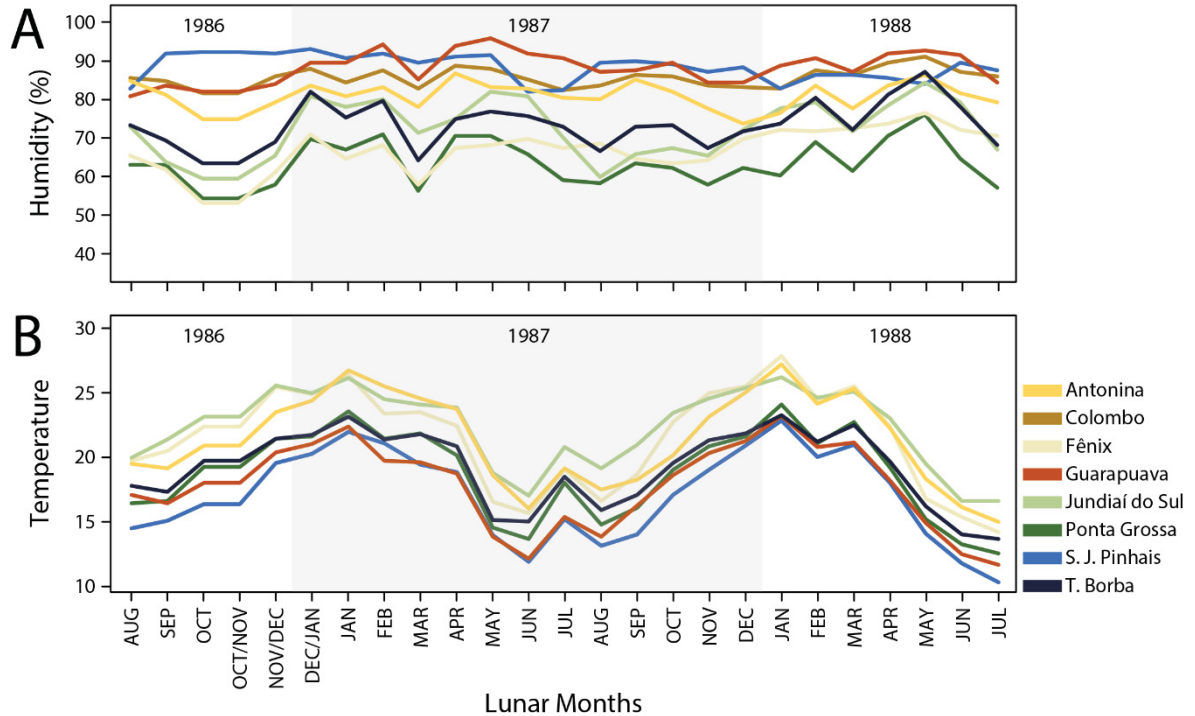


Figure 2 – **A**, Novilunium relative humidity per month and **B**, Novilunium average minimum temperature (C°) per month from August 1986 to July 1988 for each locality.

4.3 ANALYSES

Mating flight phenology was identified by circular statistical tools and visually by inspecting the graphs and tables. Circular analyses were used in order to test whether the army ant flights are temporally structured. In this method, the date of capture of each specimen is transformed into degree values ranging from 0 to 360°, in which the “0” value established as 1st January (Zar, 2010). Thus, the phenological occurrence dates are transformed to an angle proportional to the circularity of the 365 days in a year. We first calculated the mean angle vector (μ) and its standard deviation for each species. The Rayleigh’s Uniformity was performed to test if the abundance distribution is uniform throughout the year (Bergin, 1991; Ribeiro *et al.*, 2010). After rejecting the hypothesis of uniform abundances, the mean angle was used to represent the concentration of flight for a specified period of the year. We used the Watson-Williams F-test to compare differences among the mean angles among the species. Circular analyses were performed using Oriana (Kovach Computing Services, 2011).

To test the effect of temperature and humidity on species mating flight, we constructed a generalized linear mixed model (GLMMs) that accounted for species with ≥ 60 specimens (1%). As random effects, we entered the localities in order to account for spatial heterogeneity on sampling units. As fixed effects, we entered the average minimum temperature and the relative humidity. In order to test the climatic conditions on the day of the flight and prior to the flight we entered, those variables were divided as: **(1)** the average minimum temperature and the relative humidity of the five days of sampling, considering this scenario as accounting for factors related to the flight start; **(2)** the average minimum temperature and the relative humidity of 30 days prior to sampling, considering this scenario as accounting for factors related to the development of the males; and, **(3)** the average minimum temperature and the relative humidity of the 60 days prior to sampling, considering this as accounting for factors related to the pre-reproduction season and development of the males (Table 1). The abundance of ants per new moon was entered as the response variable.

The effects of the fixed variables were evaluated by comparing concurrent models (models constructed by sequentially deleting the effect of interest) using the Akaike Information Criterion (AIC). Smaller values of AIC are indicative of a better-fitting model, and we used Δ AIC values to compare support in the data for each model. When comparing two models, a Δ AIC value of less than two indicates substantial support for both models (Burnham *et al.*, 2011). In addition, a null model was added using random values, resulting in a total of 25 models for each species (Table 1). Correlation analyses (Pearson's r , R Core Team 2019) were used to check for collinearity between the environmental variables used in the GLMMs. No pair of variables showed a correlation greater than 0.5 (Pearson's correlation). Models were generated assuming Poisson distribution and using the `lm4` package (Bates *et al.*, 2012) in the R environment version 3.6.1 (R Core Team 2019).

Table 1 – Summary of the GLMMs models fitted and used in the model selection procedure for each ant species.

Code Number	Model variables	Interpretation
1	Temperature 5 + Humidity 5	Response to day-of-flight temperature and humidity
2	Temperature 5 + Humidity 30	Response to day-of-flight temperature and 30 days pre-flight humidity
3	Temperature 5 + Humidity 60	Response to day-of-flight temperature and 60 days pre-flight humidity
4	Temperature 30 + Humidity 5	Response to 30 days pre-flight temperature and day-of-flight humidity
5	Temperature 30 + Humidity 30	Response to 30 days pre-flight temperature and humidity
6	Temperature 30 + Humidity 60	Response to 30 days pre-flight temperature and 60 days pre-flight humidity
7	Temperature 60 + Humidity 5	Response to 60 days pre-flight temperature and day-of-flight humidity
8	Temperature 60 + Humidity 30	Response to 60 days pre-flight temperature and 30 days pre-flight humidity
9	Temperature 60 + Humidity 60	Response to 60 days pre-flight temperature and humidity
10	Temperature 5	Response to day-of-flight temperature
11	Temperature 30	Response to the temperature of 30 days pre-flight
12	Temperature 60	Response to the temperature of 60 days pre-flight
13	Humidity 5	Response to day-of-flight humidity
14	Humidity 30	Response to the humidity of 30 days pre-flight
15	Humidity 60	Response to the humidity of 60 days pre-flight
16	Null model	No climate effects

5 RESULTS

During the 884 nights sampled, the light traps yielded 6330 males belonging to 22 army ants species. They belong to the genera *Eciton* (three species), *Labidus* (three species), *Neivamyrmex* (14 species) and *Nomamyrmex* (two species). *Neivamyrmex* had the highest abundance, with 60.1% of all individuals collected. *Labidus* and *Nomamyrmex* were the second and third most abundant genera, with 18.3% and 16.3% respectively, lastly *Eciton* with 5.3% (Table 1). Species richness among the localities ranged from nine species in Antonina, Telêmaco Borba, and São José dos Pinhais, reaching 14 species in Jundiá do Sul. The average richness was around 10 species per locality.

Nine species, *Labidus mars* (Forel); *Neivamyrmex carinifrons* Borgmeier; *Neivamyrmex clavifemur* Borgmeier; *Neivamyrmex detectus* Borgmeier; *Neivamyrmex hopei* (Shuckard); *Neivamyrmex jerrmanni* (Forel); *Neivamyrmex klugi* (Shuckard); *Neivamyrmex latiscapus* (Emery); and *Neivamyrmex punctaticeps* (Emery) are recorded for Paraná for the first time. With exception of *Ne. punctaticeps*, the above-mentioned species are also new records for southern Brazil.

Neivamyrmex jerrmanni was the most abundant species across all the localities with 28% of sampled individuals (1748 individuals), *Ne. cf. iheringi* made up approximately 16% (1030) followed by *Nomamyrmex hartigii* with 15% (974). Nine other species were present in lower density (<1%): *Ne. carinifrons*, *Ne. hetschkoi*, *Ne. hopei*, *Ne. klugi*, *Ne. latiscapus*, *Ne. punctaticeps*, *Ne. cf. sulcatus*, *Ne. swainsoni*, and *Nomamyrmex esenbeckii*. *Neivamyrmex swainsoni* was recorded as a doubleton, caught only in the November/December novilunium, 1986, at Fênix.

5.1 TEMPORAL PATTERNS

Males of army ants were collected almost during the whole year, with species number per novilunium varying from one to six. Most were flying from October to April (Figure 1), where this period appears divided in October/November and March/April. The increased species number is mostly due to *Neivamyrmex*, which has the mating activity concentrated in these months. From June to September, males of *Neivamyrmex* were absent and the number of species strongly decreased.

Most of the species exhibited uniform abundances distributions throughout the year having one flight peak per year (Table 4). The mean circular vector (μ) and the circular standard deviation are described in detail in Table 2 for all species in each locality. The non-significant values from the Rayleigh's Uniformity test were mainly related to the occasional poor numbers of specimens captured.

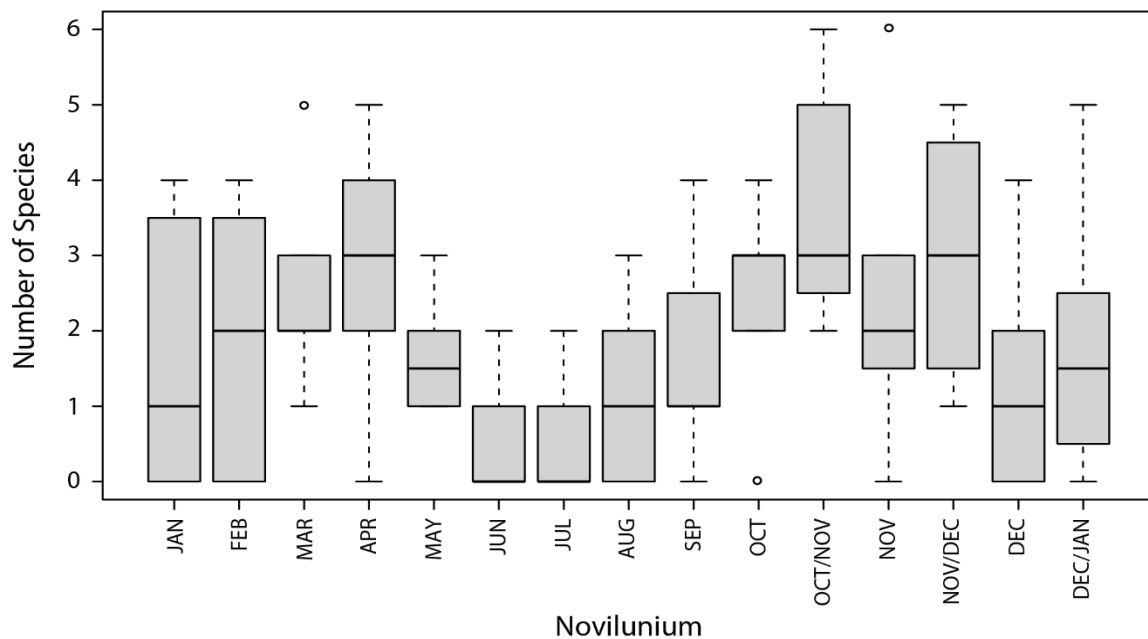


Figure 3 – Total number of species of army ant males sampled per noviluniums in the two years at the eight localities.

The *Eciton* species studied here exhibited a broad range of segregation in flight activity as can be seen by comparing the mean angle vector (see Table 2 and Figure 4). *E. burchellii* has most flight activity during one month per year in Colombo, but up to three months in Antonina and São José dos Pinhais. Overall the flight range is from October to May with few species sampled in August and September in Antonina, 1987. *Eciton quadriglume* has a more restricted period of mating flight, ranging from March to April, while *E. vagans dubitatum* has flight activities from December to January. A summary of army ant phenologies by localities and comprising the information from previous studies is presented in the supporting information (Table S2).

Labidus species are distributed along all months of the year. The species show segregation in flight activity by comparing the mean angle vector (Table 3). Overall, in nearly all the localities, *L. coecus* flight takes from one to three months, usually showing a peak of abundance in one month with considerably fewer individuals in the others. In this sampling, the flight occurred from August to November (Figure 4). However, there are differences in phenology among the localities. The flight begins early in Antonina, around July/August, followed by Colombo in August/September. In Telêmaco Borba and Jundiá do Sul the flight period begins in August and extends to October. In Fênix it begins in September/October, followed by São José dos Pinhais in October and finally in Guarapuava, with flight activities beginning in November, though a few individuals were sampled from April to August. In Ponta

Grossa, the flight lasted more than six months for both years, ranging from July to December, with fewer individuals flying among April and May. *Labidus mars* have a relatively restrict flight period of no more than two months a year. Their males take to the air from August to October, though one individual was sampled in July in Antonina. *Labidus mars* and *L. coecus* have partially overlapping phenologies, as both species were sampled together on the same night, however, the mean angle between them is different (Table 3). *Labidus praedator* shows elevated flight activity in a month, with fewer specimens flying in the month before or after, with most activity from March to June. However, different phenology is found in Fênix and Jundiáí do Sul, with a broader flight period that begins earlier, starting in October and extending until June. Though in the first year in Jundiáí do Sul the flight occurred only in November and December.

Table 2 – Summary of Watson-Williams F-tests results comparing differences among the mean angle of *Eciton* species.

	<i>E. burchellii</i>	<i>E. quadriglume</i>	<i>E. vagans dubitatum</i>
<i>E. burchellii</i>	-		
<i>E. quadriglume</i>	< 0.001	-	
<i>E. vagans dubitatum</i>	< 0.001	< 0.001	-

Table 3 - Summary of Watson-Williams F-tests results comparing differences among the mean angles of *Labidus* species.

	<i>L. coecus</i>	<i>L. mars</i>	<i>L. praedator</i>
<i>L. coecus</i>	-		
<i>L. mars</i>	< 0.001	-	
<i>L. praedator</i>	< 0.001	< 0.001	-

Table 3 – Descriptive statistics derived from circular analysis of the abundance of army ants collected during two years with light traps for five days at each new moon. $\mu_0 = 1^{\text{st}}$ Jan.

Species	Antonina			Colombo			Fenix			Guarapuava			Jundiá do Sul			Ponta Grossa			São José dos Pinhais			Télemaco Borba				
	N	μ	CSD	N	μ	CSD	N	μ	CSD	N	μ	CSD	N	μ	CSD	N	μ	CSD	N	μ	CSD	N	μ	CSD		
<i>Eciton burchellii</i>	59	333°	36°	**	1	56°	-	-	-	0	-	-	0	-	-	0	-	-	19	38°	50°	**	0	-	-	
<i>Eciton quadriglume</i>	7	112°	10°	**	8	115°	7°	**	-	0	-	-	0	-	-	13	100°	9°	**	70	93°	15°	**	14	109°	8°
<i>Eciton vagans dubitatum</i>	0	-	-	-	0	-	-	-	**	20	5°	19°	**	0	-	-	-	-	0	-	-	-	0	-	-	
<i>Labidus coecus</i>	74	231°	8°	**	39	250°	12°	**	**	144	273	11	**	176	292	50	**	**	54	279°	61°	**	22	272°	4°	**
<i>Labidus mars</i>	1	194°	-	-	5	254°	15°	**	-	0	-	-	-	4	233°	1°	**	**	39	241°	14°	**	35	251°	13°	**
<i>Labidus praedator</i>	209	141°	21°	**	11	90°	15°	**	**	74	125	87	**	18	103°	26°	**	**	11	96°	11°	**	9	117°	0°	**
<i>Neivamyrmex carinifrons</i>	1	146°	-	-	0	-	-	-	-	0	-	-	-	0	-	-	-	-	0	-	-	-	11	114°	17°	**
<i>Neivamyrmex clavifemur</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	61	38°	11°	**	-	0	-	-	-	0	-	-	
<i>Neivamyrmex detectus</i>	0	-	-	-	49	48°	20°	**	**	47	39°	32°	**	26	360°	28°	**	**	144	54°	20°	**	1	104°	-	-
<i>Neivamyrmex halidaii</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	41	329°	10°	**	**	0	-	-	-	125	317°	14°	**
<i>Neivamyrmex hetschkoii</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	3	87°	2°	0.03	**	0	-	-	-	0	-	-	
<i>Neivamyrmex hopei</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	18	323°	16°	**	**	0	-	-	-	0	-	-	
<i>Neivamyrmex iheringi</i>	0	-	-	-	0	-	-	-	**	594	51°	28°	**	0	-	-	-	**	0	-	-	-	0	-	-	
<i>Neivamyrmex jerrmanni</i>	0	-	-	-	572	109°	14°	**	**	0	-	-	-	174	104°	22°	**	**	329	89°	22°	**	6	111°	6°	**
<i>Neivamyrmex klugi</i>	0	-	-	-	0	-	-	-	**	41	330°	14°	**	0	-	-	-	-	0	-	-	-	0	-	-	
<i>Neivamyrmex laticapax</i>	0	-	-	-	0	-	-	-	**	8	328°	5°	**	0	-	-	-	**	0	-	-	-	0	-	-	
<i>Neivamyrmex piraticus</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	0	-	-	-	**	223	21°	17°	**	0	-	-	
<i>Neivamyrmex punctaticeps</i>	6	342°	16°	**	1	303°	-	-	0.03	3	328°	5°	0.03	1	328°	-	-	-	0	-	-	-	0	-	-	
<i>Neivamyrmex sulcatus</i>	0	-	-	-	0	-	-	-	-	0	-	-	-	4	84°	5°	**	**	6	46°	15°	**	0	-	-	
<i>Neivamyrmex swainsoni</i>	0	-	-	-	0	-	-	-	-	2	302°	-	0.13	0	-	-	-	-	0	-	-	-	0	-	-	
<i>Nomamyrmex esenbeckii</i>	16	280°	17°	**	1	272°	-	-	**	15	287°	21°	**	0	-	-	-	**	5	313°	14°	**	0	-	-	
<i>Nomamyrmex hartigii</i>	72	288°	17°	**	35	306°	13°	**	**	27	279°	15°	**	394	292°	18°	**	**	309	255°	42°	**	4	304°	12°	0.01

N, ants abundance; μ , mean circular vector; CSD, circular standard deviation; R, Rayleigh's Uniformity test **<0.01 Significant values.

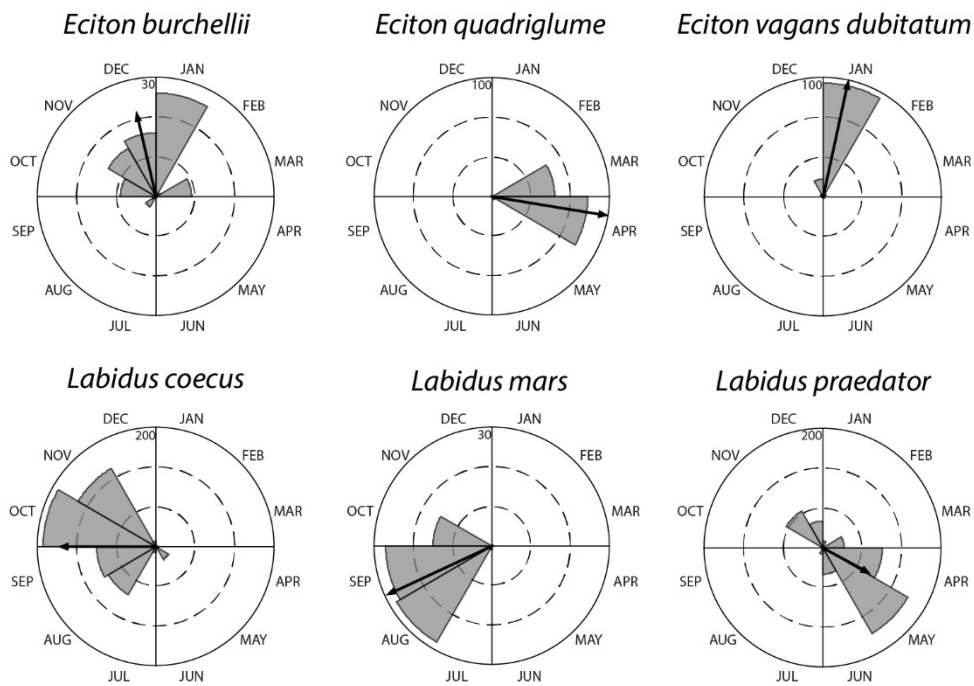


Figure 4 – Circular histograms of the abundance of *Eciton* and *Labidus* species sampled during two years for the eight localities. The arrows represent the mean angle, its length represents the phenology intensity exhibited; gray bars represent the total abundance in each month; the number represents the higher value of the abundance scale.

The species of *Neivamyrmex* studied here exhibited similar patterns in their phenologies, generally ranging from one to two months of flight activities, with few species reaching three months. *Neivamyrmex* species tend to have similar phenologies between localities and years with flights generally occurring from October to April (Table 4, Figure 5), with a few individuals of *Ne. hetsckoi* sampled in May. Flight activities of *Ne. halidaii*, *Ne. hopei*, *Ne. klugi*, *Ne. latiscapus*, *Ne. punctaticeps*, and *Ne. swainsoni* are mostly from November to December. Though a few individuals of *Ne. halidaii* and *Ne. latiscapus* were sampled in October. The flight of *Ne. punctaticeps* might extend until January. *Neivamyrmex piraticus* flew from December to February, with a conspicuous peak in January. *Neivamyrmex clavifemur*, *Ne. detectus*, *Ne. cf. iheringi*, and *Ne. cf. sulcatus* flew from January to March. *Neivamyrmex carinifrons*, *Ne. hetsckoi*, and *Ne. jerrmanni* are later species with flights from March to April, extending to May in *Ne. hetsckoi*. The summary of the Watson-Williams F-test can be seen in Table 5.

The flight phenology of the two *Nomamyrmex* species are almost overlaid (Table 4, Figure 5), with their respective mean angles not statistically different ($p = 0.09$). Both species flew mostly in October and November, having been collected on the same night. *Nomamyrmex esenbeckii* flew mostly for two months of the year, ranging from September to December, with

most individuals sampled in October. *Nomamyrmex hartigii* also flew mostly during October and November, although individuals were sampled in August 1986 in Ponta Grossa, and in December 1986 in Colombo.

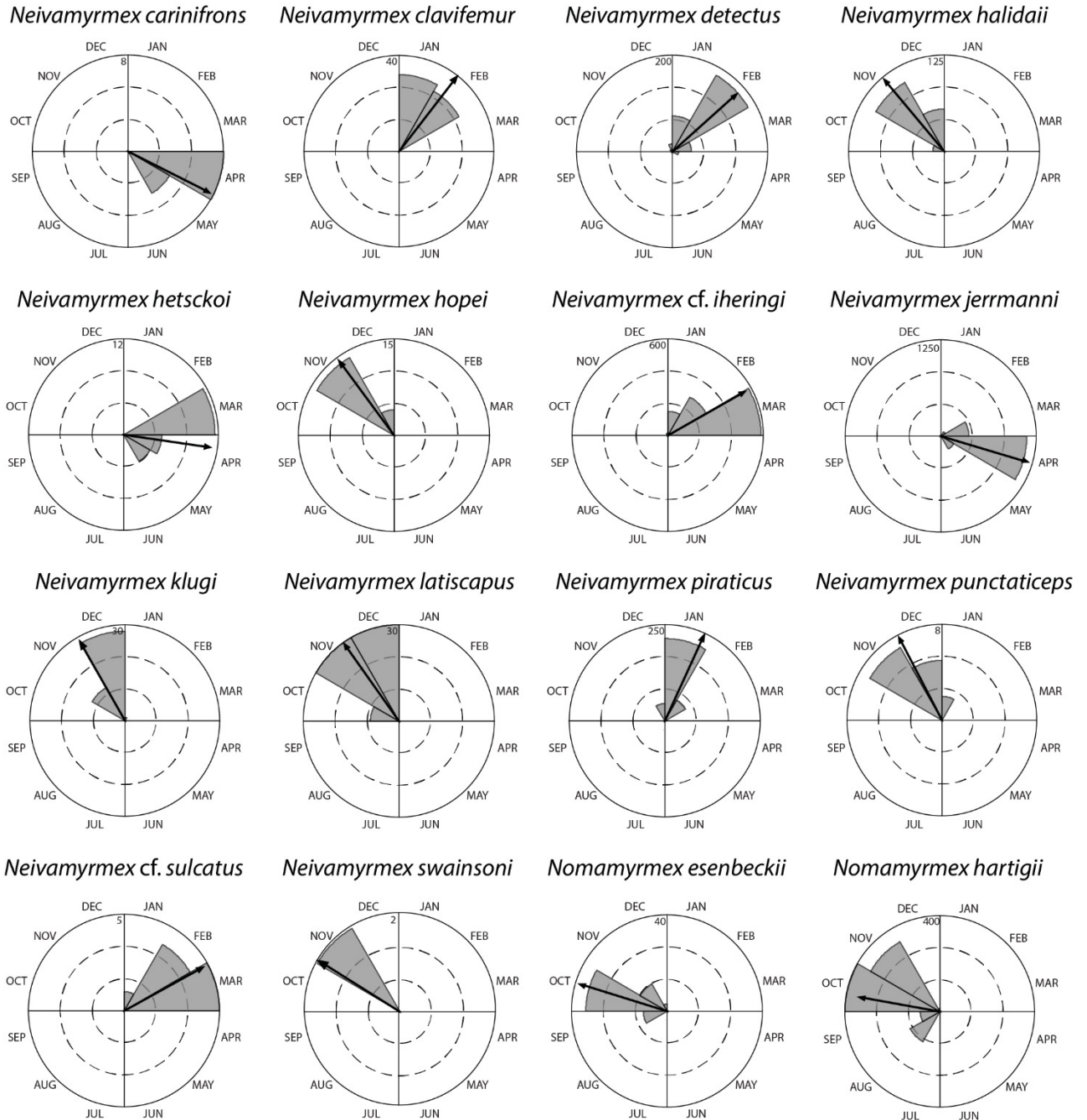


Figure 5 – Circular histograms of the abundance of *Neivamyrmex* and *Nomamyrmex* species sampled during two years for the eight localities. The arrows represent the average vector length (r), its length represents the phenology intensity; gray bars represent the total abundance in each month; the number represents the highest value of the abundance scale.

Table 2 - Summary of the Watson-Williams F-test results comparing the differences among the mean angles of *Neivamyrmex* species. Bold values represent equal mean angles ($p = 0.01$).

	<i>Ne. cariniifrons</i>	<i>Ne. clavifemur</i>	<i>Ne. detectus</i>	<i>Ne. halidaii</i>	<i>Ne. hetschkoi</i>	<i>Ne. hopei</i>	<i>Ne. cf. iheringi</i>	<i>Ne. jerrmanni</i>	<i>Ne. klugi</i>	<i>Ne. laticapus</i>	<i>Ne. piraticus</i>	<i>Ne. punctaticeps</i>	<i>Ne. cf. sulcatus</i>
<i>Ne. cariniifrons</i>	-												
<i>Ne. clavifemur</i>	< 0.001	-											
<i>Ne. detectus</i>	< 0.001	0.002	-										
<i>Ne. halidaii</i>	< 0.001	< 0.001	< 0.001	-									
<i>Ne. hetschkoi</i>	0.032	< 0.001	< 0.001	< 0.001	-								
<i>Ne. hopei</i>	< 0.001	< 0.001	< 0.001	0.369	< 0.001	-							
<i>Ne. cf. iheringi</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	-						
<i>Ne. jerrmanni</i>	0.078	< 0.001	< 0.001	< 0.001	0.055	< 0.001	< 0.001	-					
<i>Ne. klugi</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.108	< 0.001	< 0.001	-				
<i>Ne. laticapus</i>	< 0.001	< 0.001	< 0.001	0.162	< 0.001	0.797	< 0.001	< 0.001	0.104	-			
<i>Ne. piraticus</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	-		
<i>Ne. punctaticeps</i>	< 0.001	< 0.001	< 0.001	0.002	< 0.001	0.118	< 0.001	< 0.001	0.602	0.084	< 0.001	-	
<i>Ne. cf. sulcatus</i>	< 0.001	< 0.001	0.136	< 0.001	< 0.001	< 0.001	0.948	< 0.001	< 0.001	< 0.000	< 0.001	< 0.001	-
<i>Ne. swainsoni</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

5.2 TEMPERATURE AND HUMIDITY ON ARMY ANT MALE ABUNDANCE

The generalized linear mixed models for males abundance indicate temperature and humidity have an important effect as a predictor variable for all species (see Table 6). However, the species were affected by different variable scales (pre-flight and day-of-flight). In this sense, three groups can be recognized:

(1) Abundance is affected by day-of-flight temperature and pre-flight humidity. The humidity during the previous 30 days to flight had a positive effect on the abundance of *E. burchellii*, *E. vagans dubitatum*, but a negative effect on *Ne. halidaii*. While temperature had a positive effect on those species. Humidity during the previous 60 days to flight and temperature of day-of-flight affected positively the abundance of *Ne. clavifemur*, *Ne. detectus*, and *Ne. cf. iheringi*.

(2) For *E. quadriglume*, *L. praedator* and *Ne. jerrmanni* abundance is affected positively by the temperature during the 60 days before the flight and by the day-of-flight humidity.

(3) Species affected by pre-flight temperature and pre-flight humidity. *Labidus mars*, *Ne. piraticus*, and *No. hartigii* were affected by the temperature during the 30 days before the flight temperature and humidity during the 60 days before the flight. The temperature and humidity had a positive effect only for *Ne. piraticus* while a negative effect on *L. mars* and *No. hartigii*. *Labidus coecus* and *No. esenbeckii* were negatively affected by the 60 days of pre-flight temperature and humidity

Table 3 – Results of selected generalized mixed models (GLMM) investigating the effect of temperature and humidity on the male abundance in eight localities in Paraná. The table shows the estimated coefficients for the linear model for each variable (\pm standard error) and the results of the likelihood ratio test.

Selected Model				
<i>Eciton burchellii</i>	Estimate	Standard error	X^2	P
Intercept	-10.434	2.854		
Temperature NM+Humidity 30			43.118	<0.001*
Temperature NM	5.148	0.937	-	-
Humidity 30	3.114	1.431	-	-
<i>Eciton quadriglume</i>	Estimate	Standard error	X^2	P
Intercept	-9.2898	1.2135		
Temperature 60+Humidity NM			94.009	<0.001*
Temperature 60	6.6049	0.7579	-	-
Humidity NM	5.1628	0.9195	-	-
<i>Eciton vagans dubitatum</i>	Estimate	Standard error	X^2	P
Intercept	-32.342	5.470		
Temperature NM+Humidity 30			258.86	<0.001*
Temperature NM	25.385	3.028	-	-
Humidity 30	6.032	0.965	-	-
<i>Labidus coecus</i>	Estimate	Standard error	X^2	P
Intercept	8.579	0.928		
Temperature 60+Humidity 60			744.39	<0.001*
Temperature 60	-5.761	0.334	-	-
Humidity 60	-10.253	0.526	-	-
<i>Labidus mars</i>	Estimate	Standard error	X^2	P
Intercept	5.868	0.943		
Temperature 30+Humidity 60			101.79	<0.001*
Temperature 30	-8.686	1.216	-	-
Humidity 60	-8.056	1.416	-	-
<i>Labidus praedator</i>	Estimate	Standard error	X^2	P
Intercept	-4.275	0.616		
Temperature 60+Humidity NM			275.9	<0.001*
Temperature NM	1.367	0.275	-	-
Humidity NM	5.513	0.384	-	-
<i>Neivamyrmex clavifemur</i>	Estimate	Standard error	X^2	P
Intercept	-57.802	10.399		
Temperature NM+Humidity 60			85.63	<0.001*
Temperature NM	32.638	9.985	-	-
Humidity 60	25.975	4.485	-	-
<i>Neivamyrmex detectus</i>	Estimate	Standard error	X^2	P
Intercept	-16.681	1.617		
Temperature NM+Humidity 60			53.979	<0.001*
Temperature NM	13.917	0.972	-	-
Humidity 60	9.599	0.721	-	-
<i>Neivamyrmex halidaii</i>	Estimate	Standard error	X^2	P
Intercept	-2.596	0.001		
Temperature NM+Humidity 30			218.92	<0.001*
Temperature NM	3.393	0.001	-	-
Humidity 30	-12.94	0.001	-	-
<i>Neivamyrmex cf. iheringi</i>	Estimate	Standard error	X^2	P
Intercept	-25.672	3.871		
Temperature NM+Humidity 60			1859	<0.001*
Temperature NM	11.976	0.4923	-	-
Humidity 60	7.969	0.3616	-	-

<i>Neivamyrmex jerrmanni</i>	Estimate	Standard error	X^2	P
Intercept	-8.230	1.872		
Temperature 60+Humidity NM			1617.4	<0.001*
Temperature 60	6.188	0.219	-	-
Humidity NM	4.167	0.217	-	-
<i>Neivamyrmex piraticus</i>	Estimate	Standard error	X^2	P
Intercept	-33.055	5.2945		
Temperature 30+Humidity 60			870.96	<0.001*
Temperature 30	24.545	1.9780	-	-
Humidity 60	2.682	0.7796	-	-
<i>Nomamyrmex esenbeckii</i>	Estimate	Standard error	X^2	P
Intercept	4.172	1.309		
Temperature 60+Humidity 60			5.3928	<0.001*
Temperature 60	-4.122	0.885	-	-
Humidity 60	-9.894	1.431	-	-
<i>Nomamyrmex hartigii</i>	Estimate	Standard error	X^2	P
Intercept	8.387	1.075		
Temperature 30+Humidity 60			1016.2	<0.001*
Temperature 30	-3.964	0.234	-	-
Humidity 60	-10.836	0.502	-	-

Significant effect of factor $P < 0.05$. **NM**= new moon (day-flight). **30** and **60**= 30 or 60 days previous to the new moon (pre-flight).

6 DISCUSSION

Despite its importance and interest, our understanding of ant mating flights and the environmental cues that cause them remains unsure. This is mainly because most of the studies that have explored environmental factors, in particular, the climatic factors, as triggers of ants' flights, were narrowly in space or in time (Kaspari *et al.*, 2001ab; Nascimento *et al.*, 2011; Feitosa *et al.*, 2016). The macroscale patterns could not be attended by a limited sample size and spatiotemporal scale. Thus, our data represent the first attempt to describe the flight phenology of army ants upon a regional scale and for two years. Although monthly sampling design for broad temporal and spatial scales is a complex and time-consuming task, this spatiotemporal information is critical to understand the environmental triggers of mass events, such as the ant flights (e. g. Hart *et al.*, 2017).

6.1 TEMPORAL PATTERNS

Our findings show that army ant mating flights occupy ample temporal niches, with flight period occurring in strong pulses for a few months for most species. *Eciton* and *Labidus* species exhibited highly temporal segregation on phenologies. While many *Neivamyrmex* and *Nomamyrmex* species have overlapping flight seasons (Figure 4, 5).

The segregation of flight schedules occurs among ants, either for the season of the year (Noordijk *et al.*, 2008) or the hours of the day (Boomsma & Leusink, 1981; Torres *et al.*, 2001; Feitosa *et al.* 2016). Besides, previous studies have reported similar patterns of flight segregation for some species of army ants (Baldrige *et al.*, 1980; Nascimento *et al.*, 2004; Nascimento *et al.*, 2011). It has been hypothesized that flight phenology among congeneric species could serve as an effective barrier to interspecific hybridization, but how widespread and efficient this is as an isolating mechanism among ants has not been determined (Hölldobler & Wilson, 1990).

Segregation between the mating flights of *Labidus coecus* and *L. praedator* has been reported by Nascimento *et al.* (2004, 2011), and we found the same pattern in Paraná state. However, even with the flight peaking in different months throughout the year between the species, we sampled a few individuals of both species during the same new moon in five localities: in March, Ponta Grossa; April, Guarapuava; July, Antonina; and November, Fênix and Jundiáí do Sul. These individuals could have been either at the beginning or at the end of the mating period, thus a short period of overlap may occur. Alternatively, these few individuals could have been simply flying outside of the main reproductive period, as described for *E. burchellii* (Nascimento *et al.* 2011).

Mating flight for *L. coecus* and *L. praedator* seem to be later and shorter in Paraná when compared with those of Minas Gerais, Brazil (Nascimento *et al.* 2004) and Bahia, Brazil (Nascimento *et al.*, 2011) (see Table S2). In Paraná, *L. coecus* flights may begin mostly in August, or later, and usually take two months, though in some localities three months. In Minas Gerais it begins in June and lasts until September, lasting three months, and in Bahia, it starts in July until September, also lasting three months. The same occurs for *L. praedator*, as it begins to fly in April, or later, and usually takes two to three months for most Paraná localities. With the exception of Fênix and Jundiáí do Sul, where the species start to fly in November and take six months. In Minas Gerais, *L. praedator* flies from October until May, a total of eight months. In Bahia, flights start in December and last until May, a total of six months (Nascimento *et al.*, 2004; Nascimento *et al.*, 2011). Interestingly, we found *Labidus mars* flies from August to October, overlapping with *L. coecus*, but in Minas Gerais, *L. mars* flies from October to December, overlapping with *L. praedator* (Nascimento *et al.*, 2004). Apparently, the mechanism of segregation between *L. coecus* and *L. praedator* does not occur with *L. mars*.

The species of *Eciton* studied here also exhibited a mating flight period much more restricted in Paraná than in Bahia (Nascimento, *et al.*, 2011). In Bahia, *E. burchellii* flies almost the whole year with a peak from December to February, while in Paraná we found flight activity

mostly for three months ranging from October to February. Our results corroborate species having a shorter reproductive period the further they are from the tropical zones (Kaspari *et al.*, 2001). Baldrige *et al.* (1980) discuss similar patterns for army ants from the United States, with the species from Arizona having a shorter flight season than species from Texas, probably reflecting the earlier warm season in Texas. The shorter flying season of army ants in Paraná might reflect a later and shorter warm season, for example, Fênix and Jundiá do Sul have a wider warm season (Marinoni & Dutra, 1991), showing a flying season more similar to northern regions.

Neivamyrmex species have a shorter mating season when compared to other army ant genera, with the species generally flying for only a few months of the year, with an abundance peak in one new moon. The mating season seems to be restricted to the warmest months ranging from October to April, a pattern also reported for *Neivamyrmex* from Bahia, Brazil (Nascimento *et al.* 2011).

Flight segregation seems to occur in at least some species of army ants, isolating mating activity between them. However, this would be best understood by investigating whether phylogenetically related species tend to share similar phenology events or not (*e. g.* Lessard-Therrien *et al.*, 2014; Basnett *et al.*, 2019). For sympatric species with mating activity at the same month and same locality, three scenarios are possible:

(1) Existence of an isolating mechanism by flight on a time scale of fewer than 24 hours (*e. g.* Torres *et al.*, 2001; Feitosa *et al.*, 2016). Kanno (1969) reported segregation during the night for *Neivamyrmex* and Haddow *et al.* (1966) for *Dorylus*. A specific time for army ant flights during the night probably could occur but would depend upon the time of nest migration, both activities being nocturnal (Rettenmeyer, 1963). Mating flights at specific hours of the night are also known for other ant genera, as *Myrmica* (Kanno, 1959), *Pogonomyrmex* (Hölldobler, 1976), and *Leptothorax* (Plateaux, 1978).

(2) Morphology, behavior, and pheromones typically function as communication systems and mechanisms for the recognition of mates (Hölldobler and Engel-Siegel, 1982; Heinze & Buschinger, 1989; Vander Meer & Alonso, 1998). Because females are flightless and never leave their colony, males must fly between colonies and run a gauntlet of workers before approaching the female. Therefore, army ant workers potentially have control over which males will obtain access to a virgin female, perhaps by recognizing and selecting heterospecific males (Franks and Hölldobler, 1987). Morphological differences could also play a role in avoiding hybridization. Although we do not test this hypothesis, we noted that *Neivamyrmex* which has

many species flying in the same month seemed to have the largest diversity of male genital morphology (Borgmeier, 1955).

(3) Mating flights synchronized in space and time could result in hybridization among species. Morphological and genetic studies have revealed the presence of hybrids among ants (Helms Cahan *et al.*, 2002; Umphrey, 2006; Feldhaar *et al.*, 2008), including the army ant *Dorylus (Anomma)* (Kronauer *et al.*, 2011). Future work will have to investigate the patterns of the flight phenology considering the populational genetics among these species. Also, checking the ongoing gene-flow between sympatric army ants species might precisely clarify the possibility of hybridization.

6.2 CLIMATIC CORRELATES

The results of our models show that temperature and humidity are important factors impacting army ant flights, but the effects upon each species are quite different. Half of the species showed a positive response to day-of-flight temperature while the other half a varied response to pre-flight temperature. Regarding the humidity, most species showed an important response to the pre-flight, but of these, half was positive and half negative. Thus, our results suggest a common positive response to day-of-flight temperature, matching with Nascimento *et al.*, (2011), but a more variable response to pre-flight humidity. These diverse responses to weather conditions are expected considering the diversity of phenologies among species, in which flights occur almost the entire year.

According to Schneirla and Brown (1952), in *Eciton* species when the colony enters a stary phase after a dry period it starts to produce the sexual-brood. Drier conditions induce a non-stimulation of the queen's sperm gland, and perhaps a lack of hydrostatic pressure needed to accomplish the fertilization of the eggs, thus the majority of eggs became males. The few young queens are produced due to sperms retained from the last brood. The sperm duct of *Eciton* queens appears to be specially adapted for retaining a few sperm between broods, constituting a lagging of sperm between their activation and entrance into the egg. This sperm-lag is critical when followed by a period of dry weather because it is responsible for fertilizing the first eggs laid, all of which, became reproductive females (Flanders, 1976).

Although the prevalence of dry weather, Schneirla and Brown (1952) also found that colonies that became stary at the same time but enter more humid sites tend to produce worker broods. Besides that, sexual-broods were found in the wet-season but in low numbers (Schneirla & Brown, 1952). The answer apparently depends upon a species and population differences

with more broadly effects to environmental triggers (e.g. Califano & Chaves-Campos, 2011). For example, Kanno (1969) reported *Nomamyrmex* and *Labidus* species flying after a dry and cold period in Panama and we found the same for *L. coecus*, *L. mars*, *No. esenbeckii* and *No. hartigii* in Paraná. But on the contrary, in our data *Eciton* species showed a positive response to pre-flight humidity while a negative response in Panama.

Most of what we know about the biology of army ants, specially *Eciton burchellii*, comes from Barro Colorado Island in Panama (BCI). The wet and dry seasons are noticeable in BCI by the lack of rainfall on the dry season, starting early January and ending late April or May (Windsor, 1990). On the contrary, in Paraná, seasonality is more related to temperature, with most of the species having positive effects with the increase of temperature, both for the day-of-flight and before the flight. Besides that, the sexual-brood production in *Eciton* might be related to the rainfall than with the relative humidity.

7 CONSIDERATIONS

Army ants colony behavior are shaped by the cyclic process of migrations, on the nomadic phase, and nesting on the stary phase. These cyclic phases also determine brood production (Gotwald, 1995). For this reason, looking at possible regulatory conditions of the cycle processes in army ant species might help to elucidate the sexual-brood production. In this sense, is noteworthy to mention that species with epigaeic habits, as *Eciton*, tend to have a more irregular and longer mating period through years and localities than hypogaeic species. *Neivamyrmex* species, which tend to have hypogaeic habits, also tend to have more uniform and brief flight phenology. These differences could be caused by the adaptations and specializations brought by surface life, resulting in different responses to environmental conditions (Schneirla, 1957). That being the case, examining the stimulating effects on the cyclic process of hypogaeic species could help to elucidate their promotion to nomadism and nesting behavior, as well as the worker and sexual-brood production.

Our data encompasses a wide range of temporal and geographical scale for army ants showing a high diversity of flight phenologies for the group. Studies incorporating phylogenetic information in phenological responses is highly recommended and could not only allow clarifying the evolutionary history of traits but could also be important for prediction of phenological sensitivity to climate change (e. g. Davis *et al.*, 2010). Since climate change set pressure for range shifts on populations (Chen *et al.*, 2011; Helms and Bridge, 2017) and the high risk rely in isolated populations, especially those with limited gyne dispersal strategies are

particularly at risk (*e. g.* Gove *et al.*, 2009; Peters *et al.*, 2009), is critical to document how phenological trends vary geographically and by habitats (Forrest, 2016). Furthermore, looking into mating flight strategies would help to clarify the hazards of this critical phase in the life cycle of these ants and understand the tradeoffs of potential mechanisms of sympatric speciation.

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9 SUPPORTING INFORMATION

Table S1 – Complementary results of the generalized mixed models investigating the temperature and humidity of the day-flight and pre-day flight affecting the army ant male flight. The table presents Akaike information criteria (ΔAIC) in relation to the best fitted model (in bold). **T**= temperature; **H**= humidity; **5**= day-of-flight (new moon); **30**= 30 days previous of the new moon; **60**= 60 days previous of the new moon.

Species	Model	AIC	$\Delta AICc$	Species	Model	AIC	$\Delta AICc$
<i>Eciton burchellii</i>	T5+H5	308.5	4.03	<i>Eciton quadriglume</i>	T5+H5	601.38	85.06
	T5+H30	304.47	0		T5+H30	644.59	128.27
	T5+H60	309.18	4.71		T5+H60	649.31	132.99
	T30+H5	321.04	16.57		T30+H5	573.03	56.71
	T30+H30	324.04	19.67		T30+H30	599.08	82.76
	T30+H60	321.98	17.51		T30+H60	610.33	94.01
	T60+H5	333.38	28.91		T60+H5	516.32	0
	T60+H30	338.89	34.42		T60+H30	533.72	17.4
	T60+H60	333.96	29.49		T60+H60	546.66	30.34
	T5	307.31	2.84		T5	647.44	131.12
	T30	322.86	18.39		T30	610.55	94.23
	T60	337.22	32.75		T60	550.32	34
	H5	337.51	33.04		H5	635.32	119
	H30	345.36	40.89		H30	671.49	155.17
	H60	338.38	33.91		H60	678.37	162.05
Null	343.58	39.11	Null	677.74	161.42		

Species	Model	AIC	Δ AICc	Species	Model	AIC	Δ AICc
<i>Eciton vagans dubitatum</i>	T5+H5	348.45	55.22	<i>Labidus coecus</i>	T5+H5	2011.5	499.5
	T5+H30	293.23	0		T5+H30	1823.2	311.2
	T5+H60	349.65	56.42		T5+H60	1823.7	311.7
	T30+H5	408.08	114.85		T30+H5	1905.5	393.5
	T30+H30	412.68	119.45		T30+H30	1612	100
	T30+H60	405.36	112.13		T30+H60	1530	18
	T60+H5	398.84	105.61		T60+H5	1814	302
	T60+H30	415.59	122.36		T60+H30	1574.4	62.4
	T60+H60	344.23	51		T60+H60	1512	0
	T5	351.48	58.25		T5	2254.2	742.2
	T30	414.92	121.69		T30	2102	590
	T60	413.59	120.36		T60	1997.1	485.1
	H5	546.3	253.07		H5	2011.3	499.3
	H30	532.67	239.44		H30	1879.6	367.6
	H60	545.97	252.74		H60	1903.1	391.1
Null	548.09	254.86	Null	2252.4	740.4		
<i>Labidus mars</i>	T5+H5	273.42	51.28	<i>Labidus praedator</i>	T5+H5	1753.8	2.9
	T5+H30	258.45	36.31		T5+H30	2006.4	255.5
	T5+H60	250.46	28.32		T5+H60	1990.9	240
	T30+H5	257.4	35.26		T30+H5	1773.2	22.3
	T30+H30	237.4	15.26		T30+H30	2010.4	259.5
	T30+H60	226.52	4.38		T30+H60	2006.8	255.9
	T60+H5	246.22	24.08		T60+H5	1750.9	0
	T60+H30	226.97	4.83		T60+H30	1973.6	222.7
	T60+H60	222.14	0		T60+H60	1970.9	220
	T5	301.25	79.11		T5	2015.8	264.9
	T30	273.59	51.45		T30	2013.7	262.8
	T60	253.51	31.37		T60	1981.9	231
	H5	303.93	81.79		H5	1774.5	23.6
	H30	300.87	78.73		H30	2019	268.1
	H60	302.87	80.73		H60	2012	261.1
Null	324.3	102.16	Null	2022.8	271.9		

Species	Model	AIC	Δ AICc	Species	Model	AIC	Δ AICc
<i>Neivamyrmex clavifemur</i>	T5+H5	190.55	130.45	<i>Neivamyrmex detectus</i>	T5+H5	891.29	254.66
	T5+H30	145.73	85.63		T5+H30	690.6	53.97
	T5+H60	60.1	0		T5+H60	636.63	0
	T30+H5	124.08	63.98		T30+H5	844.87	208.24
	T30+H30	133.25	73.15		T30+H30	817.06	180.43
	T30+H60	65.9	5.8		T30+H60	754.95	118.32
	T60+H5	86.23	26.13		T60+H5	729.42	92.79
	T60+H30	86.23	26.13		T60+H30	735.69	99.06
	T60+H60	70.62	10.52		T60+H60	711.92	75.29
	T5	200.24	140.14		T5	890.87	254.24
	T30	131.25	71.15		T30	864.53	227.9
	T60	84.27	24.17		T60	752.8	116.17
	H5	245.61	185.51		H5	1315.83	679.2
	H30	266.43	206.33		H30	1241.47	604.84
	H60	228.67	168.57		H60	1231.24	594.61
Null	288.77	228.67	Null	1315.76	679.13		
<i>Neivamyrmex halidaii</i>	T5+H5	601.55	218.92	<i>Neivamyrmex cf. iheringi</i>	T5+H5	2575.2	485.9
	T5+H30	382.63	0		T5+H30	2571.6	482.3
	T5+H60	418.12	35.49		T5+H60	2089.3	0
	T30+H5	693.31	310.68		T30+H5	2787.7	698.4
	T30+H30	384.7	2.07		T30+H30	2923.4	834.1
	T30+H60	450.11	67.48		T30+H60	2570.2	480.9
	T60+H5	710.19	327.56		T60+H5	2555.7	466.4
	T60+H30	400.9	18.27		T60+H30	2758.1	668.8
	T60+H60	448.28	65.65		T60+H60	2571.2	481.9
	T5	602.23	219.6		T5	2836	746.7
	T30	702.09	319.46		T30	2962	872.7
	T60	712.3	329.67		T60	2756.3	667
	H5	709.69	327.06		H5	3465.5	1376.2
	H30	401.33	18.7		H30	3882	1792.7
	H60	450.05	67.42		H60	3690.1	1600.8
Null	713.69	331.06	Null	3944.3	1855		

Species	Model	AIC	Δ AICc	Species	Model	AIC	Δ AICc
<i>Neivamyrmex jerrmanni</i>	T5+H5	5799.9	1136.6	<i>Neivamyrmex piraticus</i>	T5+H5	860.42	377.63
	T5+H30	6058.9	1394.6		T5+H30	737.57	254.78
	T5+H60	6165.1	1500.8		T5+H60	715.97	233.18
	T30+H5	5048.2	383.9		T30+H5	489.36	6.57
	T30+H30	5337.6	673.3		T30+H30	483.63	0.84
	T30+H60	5375.1	710.8		T30+H60	482.79	0
	T60+H5	4664.3	0		T60+H5	550.37	67.58
	T60+H30	5031.6	367.3		T60+H30	565.69	82.9
	T60+H60	5044.1	379.8		T60+H60	576.28	93.49
	T5	6204.9	1540.6		T5	965.67	482.88
	T30	5395.5	731.2		T30	493.16	10.37
	T60	5044.7	380.4		T60	574.58	91.79
	H5	5874.1	1209.8		H5	1246.33	763.54
	H30	6174.5	1510.2		H30	1235.68	752.89
	H60	6171.5	1507.2		H60	1237.02	754.23
	Null	6277.7	1613.4		Null	1349.76	866.97
<i>Nomamyrmex esenbeckii</i>	T5+H5	299.83	67.2	<i>Nomamyrmex hartigii</i>	T5+H5	2464.8	342
	T5+H30	252.68	20.05		T5+H30	2463.1	340.3
	T5+H60	255.44	22.81		T5+H60	2441.5	318.7
	T30+H5	302.74	70.11		T30+H5	2449.8	327
	T30+H30	243.35	10.72		T30+H30	2226.2	103.4
	T30+H60	234.54	1.91		T30+H60	2122.8	0
	T60+H5	294.24	61.61		T60+H5	2381.3	258.5
	T60+H30	238.02	5.39		T60+H30	2214.6	91.8
	T60+H60	232.63	0		T60+H60	2125.7	2.9
	T5	319.59	86.96		T5	3077.8	955
	T30	318.17	85.54		T30	2982.1	859.3
	T60	304.99	72.36		T60	2886.6	763.8
	H5	303.03	70.4		H5	2530.4	407.6
	H30	250.89	18.26		H30	2463.7	340.9
	H60	254.95	22.32		H60	2445.2	322.4
	Null	321.67	89.04		Null	3135	1012.2

Table S2 – Summary of the seasons of male army ant flying season. In species with two lines, each one represents a year.

	Baldridge <i>et al.</i> (1980)		Kannowski (1969)		Nascimento <i>et al.</i> (2011)		Nascimento <i>et al.</i> (2014)		Tozetto, Sendoya, Latkke in prep.						
	Arizona	Texas	United States	Barro Colorado	Ilhéus	Viçosa	Fênix	Jundiá do Sul	Têlemaco Borba	Ponta Grossa	Guarapuava	S. J. dos Pinhais	Colombo	Antonina	
<i>E. burchellii</i>	-	-	-	Mar - Apr	Oct - Aug	-	-	-	-	-	-	Oct - Dec	Feb	Oct - Jan Aug-Oct	
<i>E. hamatum</i>	-	-	-	Apr - May	-	-	-	-	-	-	-	-	-	-	
<i>E. jansoni</i>	-	-	-	May	-	-	-	-	-	-	-	-	-	-	
<i>E. mexicanum</i>	-	-	-	-	Oct - Feb	-	-	-	-	-	-	-	-	-	
<i>E. quadriglume</i>	-	-	-	-	-	-	-	-	-	Apr	Apr	Mar - Apr	Apr	Apr	
<i>E. vagans</i>	-	-	-	-	Jan - Jun	-	-	-	-	Apr - May	-	Mar - Apr	Apr - May	Apr - May	
<i>E. vagans dubitatum</i>	-	-	-	-	-	-	Dec - Jan	Dec - Feb	-	-	-	-	-	-	
<i>L. coecus</i>	-	Mar - May	Mar - May	Mar - Apr	-	Jul - Sep	Oct - Nov	Sep - Nov	Aug - Nov	Apr - May	Sep - Nov ¹	Oct	Sep - Oct	Jul	
<i>L. praedator</i>	-	-	-	Mar - May	-	Oct - May	Oct - Jan, Mar - Jul	Nov - Dec	Mar - Apr	Mar	Feb - Apr	Apr	Feb - Apr	Mar - Jul	
<i>L. mars</i>	-	-	-	-	-	Oct - Dec	Dec - Jan, May - Jun	Aug	Apr	Apr	Apr - Jun	Sep - Oct	Sep - Oct	Jul	
<i>Ne. andrei</i>	Jun - Aug	-	Jun - Aug	-	-	-	-	-	Aug - Oct	Aug - Oct	-	Oct	Aug	-	

Continued in the next page.

Table S2 (Continued)

<i>Ne. Klugii</i>	-	-	-	-	May	-	-	-	Nov - Dec Nov	-	-	-	-
<i>Ne. Laticapus</i>	-	-	-	-	-	-	-	Oct - Dec	Nov - Dec Nov	-	-	-	-
<i>Ne. leptognathus</i>	-	-	-	-	-	Nov - Mar	-	-	-	-	-	-	-
<i>Ne. melshaemeri</i>	-	May - Aug	May - Aug	-	-	-	-	-	-	-	-	-	-
<i>Ne. microps</i>	-	-	-	Oct	-	-	-	-	-	-	-	-	-
<i>Ne. minor</i>	Jun - Aug	Jun	May - Sep	-	-	-	-	-	-	-	-	-	-
<i>Ne. mojave</i>	-	-	Oct	-	-	-	-	-	-	-	-	-	-
<i>Ne. nigrescens</i>	-	-	Aug - Nov	-	-	-	-	-	-	-	-	-	-
<i>Ne. pilosus</i>	-	-	-	-	-	Dec - Feb	-	-	-	-	-	-	-
<i>Ne. mandibularis</i>	Jul - Aug	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ne. pilosus mexicanus</i>	-	Jun - Aug	May - Aug	-	-	-	-	-	-	-	-	-	-
<i>Ne. piraticus</i>	-	-	-	-	-	-	Dec - Feb	Jan - Feb	-	-	-	-	-
<i>Ne. pullus</i>	-	-	-	-	May	-	Jan - Feb	Dec - Feb	-	-	-	-	-

Continued in the next page.

Table S2 (Continued)

<i>Ne. punctaticeps</i>	-	-	-	Nov - Jan	-	Dec/Nov	Nov	-	Nov	-	Nov	Dec - Jan Nov - Dec
<i>Ne. spoliator</i>	-	-	Apr - May	-	-	-	-	-	-	-	-	-
<i>Ne. sulcatus</i>	-	-	-	-	-	-	-	Jan - Feb Feb - Mar	Mar Mar	-	-	-
<i>Ne. swainsonii</i>	Jun - Aug	May - Aug	May - Sep	Nov - Feb	-	Nov	-	-	-	-	-	-
<i>Ne. texanus</i>	-	-	Sep - Nov	-	-	-	-	-	-	-	-	-
<i>No. evenbeckii</i>	-	-	Mar	Sep - Dec	-	Nov-Oct	Sep - Oct Oct - Nov	Oct - Dec	-	Oct	Oct - Nov Sep - Oct	Oct - Nov Sep - Oct
<i>No. haritigii</i>	-	-	Apr - May	-	-	Nov - Oct Oct	Sep - Nov Sep - Oct	Oct - Nov Sep - Nov ⁵	Oct - Nov Sep - Nov	Oct - Dec Oct	Oct - Nov Sep - Nov	Oct - Nov Sep - Nov

¹ Few individuals were also sampled in May

² Few individuals were also sampled in April

³ Few individuals were also sampled in April

⁴ Few individuals were also sampled in August

⁵ Few individuals were also sampled in February