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ORIGINAL ARTICLE

Army ant males lose seasonality at a site on the equator

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Abstract

Army ants are keystone predators in the tropics and subtropics. During reproduction, males fly between colonies to mate with unmated, wingless queens. The males of most species are attracted to lights, and thus their presence and the timing of reproduction can be monitored using light traps. Previous studies examined the seasonality of army ant male reproduction and its relationship to climate factors at individual sites, but less is known about variation among sites. We examined army ant male flight seasonality at three sites: (1) La Selva Biological Station in Costa Rica, a site with weak temperature seasonality and moderate rainfall and day length seasonality, (2) Yasuní National Park, Ecuador, a site with no temperature or day length seasonality and very weak rainfall seasonality, and (3) the state of Paraná in southern Brazil, a site with very strong temperature, rainfall, and day length seasonality. Army ants showed strong seasonality at the La Selva and Paraná sites, and very weak to no seasonality at the Yasuní site. At La Selva and Paraná, flight times varied among species, but were very predictable from year to year, which suggests day length or temperature as predictable cues rather than rainfall. Lack of seasonal cues near the equator may be a challenge for army ant species that need to synchronize colony reproduction, and thus may have conservation implications for minimum population sizes needed to ensure stable populations.

Abstract in Spanish is available with online material.

KEYWORDS
Alates, New World, phenology, reproduction, tropics

1 | INTRODUCTION

Phenology addresses the timing of growth and reproduction in ecological communities (Piao et al., 2019; Tang et al., 2016). Constraining effects of seasonal cold are obvious in temperate zone habitats, and effects of seasonal drought can be obvious in areas of highly seasonal rainfall. But phenological patterns become more variable, subtle, and complex in less seasonal tropical environments (Abernethy et al., 2018). Many studies of phenology emphasize plants, but phenology of consumers also receives attention (Van Schaik et al., 1993). Tropical insects exhibit a wide range of seasonal patterns, even in very weakly seasonal regions (Kishimoto-Yamada et al., 2015; Wolda, 1988). Ants are dominant consumers in tropical forests and phenology of ant reproductive flights has been measured with a variety of trapping methods (Donoso et al., 2022; Feitosa et al., 2016; Frederickson, 2006; Kaspari, Pickering, Longino, & Windsor, 2001; Kaspari, Pickering, & Windsor, 2001; Shik et al., 2013). Here we present new results on the reproductive phenology of army ants, keystone predators in tropical ecosystems.

Army ants are among the largest insect societies on Earth, with a lifestyle that combines group raiding, nomadism, permanently wingless queens, and reproduction by colony fission (Gotwald, 1995; Kronauer, 2020; Schneirla, 1971). Several ant lineages have converged on the army ant lifestyle, but members of the subfamily Dorylinae surpass all others in abundance, geographic range, and diversity. Within the Dorylinae, true army ants have evolved twice (Borowiec, 2019). One set of army ant clades has radiated in the Old World tropics, and one army ant clade occurs in the New World. The latter comprises the genera *Cheliomyrmex*, *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex* (Borowiec, 2016), which are the subjects of this study. Army ants are keystone insect predators in many regions, with multiple sympatric species that exhibit a range of prey preferences (Hoenle et al., 2019). They are of conservation concern because their large colonies and nomadic lifestyle require large areas of suitable habitat and they are sensitive to habitat fragmentation (Partridge et al., 1996; Pérez-Espona, 2021). The decline and disappearance of army ant species and populations could also provoke a similar pattern among the rich assemblages of invertebrates and vertebrates that are associated with them (Rettenmeyer et al., 2011; Kumar & O'Donnell, 2007; Peters et al., 2008; Pérez-Espona, 2021; von Beeren et al., 2021).

Army ants are well known for their synchronized brood production and clock-like alternation of nomadic and statary phases (Schneirla, 1971). The synchronization is within colonies and not among colonies, with each round of worker production requiring about 30 days (Schneirla, 1971). When sexuals are produced, it is a dedicated brood cycle in which only males and new queens are produced (at least for well-studied species *Eciton burchellii* and *E. hamatum*, and possibly for most or all army ants; Schneirla, 1948; Schneirla & Brown, 1952). Sexual production is strongly male biased, with just a few virgin queens and hundreds to thousands of males (Schneirla, 1948; Schneirla & Brown, 1952). The males are robust flying insects that are much larger than the workers and similar in size to the queens they mate with. That size similarity is both unusual and important to their biology (Franks & Hölldobler, 1987). During colony reproduction, these males fly from their home colony to a different colony, where they push their way through the workers to locate and mate with the flightless virgin queens (Gotwald, 1995). Males are rarely collected together with workers. Most species have reproductive flights at night and the males are often attracted to lights. Because many species are subterranean, have inconspicuous foraging columns, and may prefer nocturnal foraging, the presence of a species at a site can often be more easily detected with males than with workers, by monitoring lights (Basset et al., 2020). Consequently, the use of light traps has proven useful for sampling army ants and is fundamental for studies of flight phenology (Baldridge et al., 1980; Nascimento et al., 2011; Quiroz-Robledo et al., 2002; Quiroz-Robledo & Valenzuela González, 2006).

An important aspect of army ant biology is seasonality of reproduction. Multiple studies have examined seasonality of army ant males. Haddow et al. (1966) showed little seasonality in a weakly seasonal site in Uganda. Kannowski (1969) showed strong seasonality on Barro Colorado Island (BCI), Panama. BCI has a pronounced dry season, and Kannowski monitored a three-month period that was the transition from dry to wet season. Baldridge (1972) and Baldridge et al. (1980) studied temperate sites in central Texas and southern Arizona in the USA, where strong seasonality is associated with temperature and day length. One species flew in the Spring, and all other species flew in midsummer to Fall. Nascimento et al. (2011) studied a site in the Brazilian Atlantic Forest biome. The site had weak temperature seasonality and highly variable precipitation throughout the year, yet all species showed strong seasonality. Flight activity was most related to temperature, with most flying during the warmest months of the year, but one flying during the colder months. Nascimento et al. (2004) studied another site in the Atlantic Forest biome, focusing on one genus of army ants, and showed distinct seasonality and temporal segregation of three species.

Army ants occur across a full spectrum of seasonality in temperature and precipitation. Diverse army ant assemblages occur in southern North America and in southern South America, where they experience strong temperature seasonality and annual cycles of day length. In the broad tropical region, where annual temperature and day length variation is small, army ants experience a range of precipitation regimes, from desert habitats to monsoonal tropical dry forest to almost aseasonal rainforest. Seasonal patterns in the appearance of army ant males must involve (1) a cue to initiate a sexual brood, at least a month before males appear (Flanders, 1976; Schneirla & Brown, 1952); and (2) synchronization among colonies, such that many colonies initiate sexual production at approximately the same time (with some variation due to the general asynchrony of brood cycles among colonies).

Here we provide three new surveys based on quantitative light-trapping programs, one in a moderately seasonal rainforest in Costa Rica, one in a nearly aseasonal rainforest in Amazonian Ecuador, and one in the strongly seasonal state of Paraná in southern Brazil. The three surveys are highly comparable, using similar trapping methods and duration. The Costa Rican and Ecuadorian surveys were for a period of 18 months, allowing a partial assessment of interannual variability. The Paraná study was for a full two-year period. Flight seasonality is contrasted among species and sites, using the data presented here and results from previous studies.

The Costa Rican site is La Selva Biological Station, where the entire ant fauna has been extensively surveyed (Longino et al., 2002). As Supporting Information (Appendix S1), we provide here an analysis of all records of male army ants from La Selva, placing the light-trapping results in the context of the entire fauna. In the appendix we examine vertical distribution (canopy vs. ground), occurrence in different trap types (light, Malaise, flight intercept), and flight times (post-sunset vs. pre-dawn). These results provide additional insight into the behavior of male army ants.

2 | METHODS

2.1 | Study sites

2.1.1 | La Selva Biological Station, Costa Rica

This site is lowland rainforest at 10°26′N, 84°01′W (McDade et al., 1993). The station area is approximately 1500 ha. Elevation ranges from 50 to 150 m. Mean annual rainfall is approximately 4 m. The habitat is a mosaic of mature lowland rainforest, second growth forest of various ages, and abandoned pastures. Climate data for La Selva were obtained by downloading documented data files from https://tropicalstudies.org/portfolio/information-resources/ (accessed 28 Nov 2021). Downloaded files were "La Selva daily rainfall, 1963-2016 (January 2017 DA Clark).xlsx" and "LS daily T-air mean-max-min Apr1982-Dec2016 (Feb 2017).xlsx."

2.1.2 | Yasuní, Ecuador

This site was the Estación Científica Yasuní (ECY), which is maintained by Pontificia Universidad Católica del Ecuador and located within the Parque Nacional Yasuní (0°40′27″S, 76°23′50″W). The Yasuní forest is among the most diverse forests in the world, with 1104 tree species recorded in 25 ha (Valencia, Condit, et al., 2004; Valencia, Foster, et al., 2004). Yasuní is the wettest and least seasonal region of the Amazon, with a mean annual rainfall of 2826 mm, and no dry months (having <100 mm of rainfall; Valencia, Condit, et al., 2004; Valencia, Foster, et al., 2004). Elevation ranges from 220 to 260 m. The habitat consists of primary forest, with small clearings near the ECY. We used on-site climate data from the weather station maintained by ECY, including daily mean, minimum, and maximum air temperature; and daily rainfall collected from a manual rain gauge.

2.1.3 | Brazil, Paraná

The data in the Paraná study were obtained from the *Levantamento da Fauna Entomológica no Estado do Paraná* project (PROFAUPAR-UFPR). Aiming to sample areas representing the diverse environments of Paraná State, the PROFAUPAR project sampled insects in eight localities distributed from −23.4333 to −25.6667° latitude and in a variety of habitats (Table S1). Detailed descriptions of each locality can be found in Marinoni and Dutra (1991). Monthly temperature and rainfall data were available for each site, recorded at or near each site during the study. Long-term averages for each site were obtained from WorldClim version 2.1, with monthly averages for the period 1970–2000 (Fick & Hijmans, 2017).

For seasonal terminology, Paraná can use temperate zone terms Spring, Summer, Fall, Winter, with Summer being warm and wet, Winter being cold and dry. La Selva uses terms wet and dry season, with dry season being January to May. Season terms hardly apply to Yasuní, but there is a brief wet season.

2.2 | Light-trapping

Details of light trap design and operation are in Supporting Information, Appendix S2. At La Selva, sampling occurred for 18 months, from January 1998 to June 1999. Traps were run at six locations in mature forest. The two most widely separated locations were 2.3 km apart; the two closest were 335 m apart. At each location a pair of traps were run, one suspended in the canopy ~20 m high, and one on the ground beneath it. On each night of sampling, one trap pair was run. Trapping was carried out on two or three nights per week, rotating among 6 locations, resulting in an average of 21 "trap nights" (one trap for one night) per month. At Yasuní, sampling occurred for 17 months, from October 2018 to February 2020. One trap was operated for 4 nights per month during the new moon cycle (<10% illumination), resulting in four trap nights per month. In Paraná, sampling occurred for 24 months, from August 1986 to July 1988 (sampling at one site did not begin until September 1986). At each of the eight sites, traps were run for five consecutive nights during each lunar period, with the median day being the new moon. Thus, there was an average of 40 trap nights per month (5 nights × 8 sites).

2.3 | Identification

Specimens were identified using taxonomic keys, descriptions, and illustrations provided by Borgmeier (1955) and Watkins (1976), as well as comparing them with other specimens deposited in research collections or images provided by www.antweb.org. Specimens from the Costa Rica and Ecuador sites are deposited in the National Museum of Costa Rica (former INBio collection), the University of Costa Rica, and the research collection of Longino. Specimens from the PROFAUPAR project are deposited in the Padre Jesus Santiago Moure Insect Collection, Departamento de Zoologia, Universidade Federal do Paraná, Brazil. All specimens are also reported on AntWeb, with images of at least one specimen of each species from each site.

The taxonomy of the New World army ants is only partially known, and it is known that many widespread nominal species contain a diversity of divergent genotypic clusters and will ultimately resolve into mosaics of subtly different or even indistinguishable cryptic species (Barth et al., 2015; unpub. data). Thus, in this study, "species" that have broad ranges and occur at multiple sites should be understood as clades, with an unknown degree of genetic distance or reproductive isolation among sites.

2.4 | Analysis

We relied on incidence data, with replicates being individual traps on individual nights (trap nights), with the exception of three samples from Yasuní in which the samples from a 4-night sampling period were pooled. Species occurrence data were described and compared using

Circular Statistics, implemented in the R package Circular (Agostinelli & Lund, 2022). Circular Statistics are techniques for data on an angular scale, for which there is no true zero (Morellato et al., 2010). For example, values of 1° and 359° have a mean of 0° instead of 180°. Circular statistics are often applied to seasonal data like ours, in which dates are transformed to angles from 0–360°. Dispersion is measured as *rho*, which varies from 0 for evenly dispersed dates to 1 for all values concentrated in a single date. Significant seasonality (non-uniform distribution of occurrences during the year) is tested with Rayleigh tests. For our results we back-transform means to dates and report *rho* values and Rayleigh tests.

3 | RESULTS

3.1 | Comparative climate patterns

The three sites vary in latitude: Yasuní near the equator, La Selva ~10°N, and Paraná ~24°S. Day length is nearly invariant at Yasuní, varies by an hour at La Selva, and by three hours at Paraná. Temperature seasonality is nearly absent at Yasuní, very modest at La Selva, and strong in Paraná (Figures 1 and 2). Yasuní monthly rainfall varies from approximately 200–400 mm, with a unimodal peak constituting a short wet season. La Selva monthly rainfall varies from roughly 200–550 mm, with a short dry season and a prolonged, somewhat bimodal wet season. Paraná monthly rainfall varies from roughly 70–200 mm, with a wet season in the warmest months.

Observed temperature during the years of the studies closely tracked the long-term averages (Figure 1). Observed rainfall during the studies was much more variable and did not track long-term averages as closely (Figure 1). At Yasuní and La Selva, the observed values of temperature and rainfall during the overlapping portions of the first and second years of the study were not correlated, albeit sample sizes were low ($n = 5$ months for Yasuní, 6 months for La Selva). In contrast, these values were significantly correlated in the Paraná study ($n = 12$ months): Pearson correlation coefficients for minimum and maximum temperature were = >0.9, and for rainfall it was 0.66. When testing just the first six months of each year, to make sample size similar to the Yasuní and La Selva studies, correlation among the temperature variables remained high and significant, while correlation for rainfall was less and not significant.

3.2 | Male flight seasonality

At La Selva Biological Station, the quantitative light trap program captured 17 species in 233 occurrences. The Yasuní sampling captured 16 species in 82 occurrences. The extensive Paraná sampling, over eight sites, captured 22 species in 865 occurrences (Table 1).

Overall flight activity was measured as the average number of species per trap night (average summed incidence per trap night) (Figure 3). At La Selva, flight activity was concentrated during the transition from dry season to wet season. The *rho* value was 0.62 and the Rayleigh test highly significant ($p < .001$). Yasuní showed a somewhat broader distribution, yet still with a peak of activity preceding the short wet season. The *rho* value was 0.21 and the Rayleigh test weakly significant ($p < .05$). Paraná had a bimodal distribution, with flight activity very low in Winter, peaks in Spring and Fall, and intermediate in Summer. The *rho* value was 0.25, the low value reflecting the broad occurrence of flight dates, but the Rayleigh test was highly significant ($p < .001$).

Flight seasonality of individual species varied within and among sites (Table 1, Figures 4–6). La Selva and Paraná sites showed strong seasonality in male flight times; Yasuní had much lower seasonality (Figure 7). Median *rho* values (dispersion of flight times, 0 = evenly dispersed, 1 = perfectly synchronized) were above 0.9 for year 1 at La Selva and the two separate years of the Paraná study, and 0.73 for year 1 at Yasuní. This difference was significant, 1-way ANOVA, $F(3, 61) = 6.415$, $p < .001$. At La Selva, 11 of 15 species captured during year 1 had significant Rayleigh tests (a test of clustering of flight dates, see Table 1). At Paraná, 20 of 22 species were significantly clustered in year 1, 18 of 21 in year 2. At Yasuní, only 4 of 16 species showed significant clustering.

In Paraná, the most seasonal of the sites, mean species flight times were very strongly correlated between the two years (Pearson *R* .97, $p < .0001$). Many species very predictably appeared at the same time each year, and species were often staggered with respect to each other (Figure 6). The three *Eciton* species had staggered flight dates, with *E. burchellii* in early Summer, *E. vagans* in middle Summer, and *E. quadriglume* in late Summer. *Eciton burchellii* had a broader flight season than the other two. All three *Labidus* species were abundant and showed significant clustering. Although *L. praedator* and *L. coecus* had significant clustering, they had very broad flight seasons (*rho* values *L. praedator* 0.5011 and 0.5269; *L. coecus* 0.7482 and 0.6552; for years 1 and 2, respectively). Peak flight season for *L. praedator* was Fall, for *L. coecus* it was Spring. *Labidus mars* flew in Spring, like *L. coecus*, but with a shorter flight season (*rho* = 0.9561 and 0.9064; for years 1 and 2, respectively). The 14 *Neivamyrmex* species all flew in the warmer months, each with a short flight season. One group of species had mean flight days in early Summer, and another group in late Summer, reflecting the overall bimodal flight activity (Figure 3). The two *Nomamyrmex* species both showed significant clustering, and both flew in early Summer, earlier than any of the *Neivamyrmex* and overlapping with *Labidus*.

La Selva was considerably less seasonal than Paraná, yet had strong army ant seasonality (Figure 4). Nearly all species showed strong clustering in La Selva's dry season, especially during the late dry season and the transition to wet season. This applied to the three *Eciton* species, most of the *Neivamyrmex* species, and the two *Nomamyrmex* species. *Labidus coecus*, the only common *Labidus* at the site, was anomalous, flying throughout the year. Although there was significant clustering, the significance level was weak ($p < .047$) and *rho* was very low (0.35). *Neivamyrmex digitistipus* occurred once, in a mid-wet season sample. This species occurs more often in Malaise samples (see Appendix S1) and has been collected during various times of year using other methods. *Neivamyrmex fumosus* is

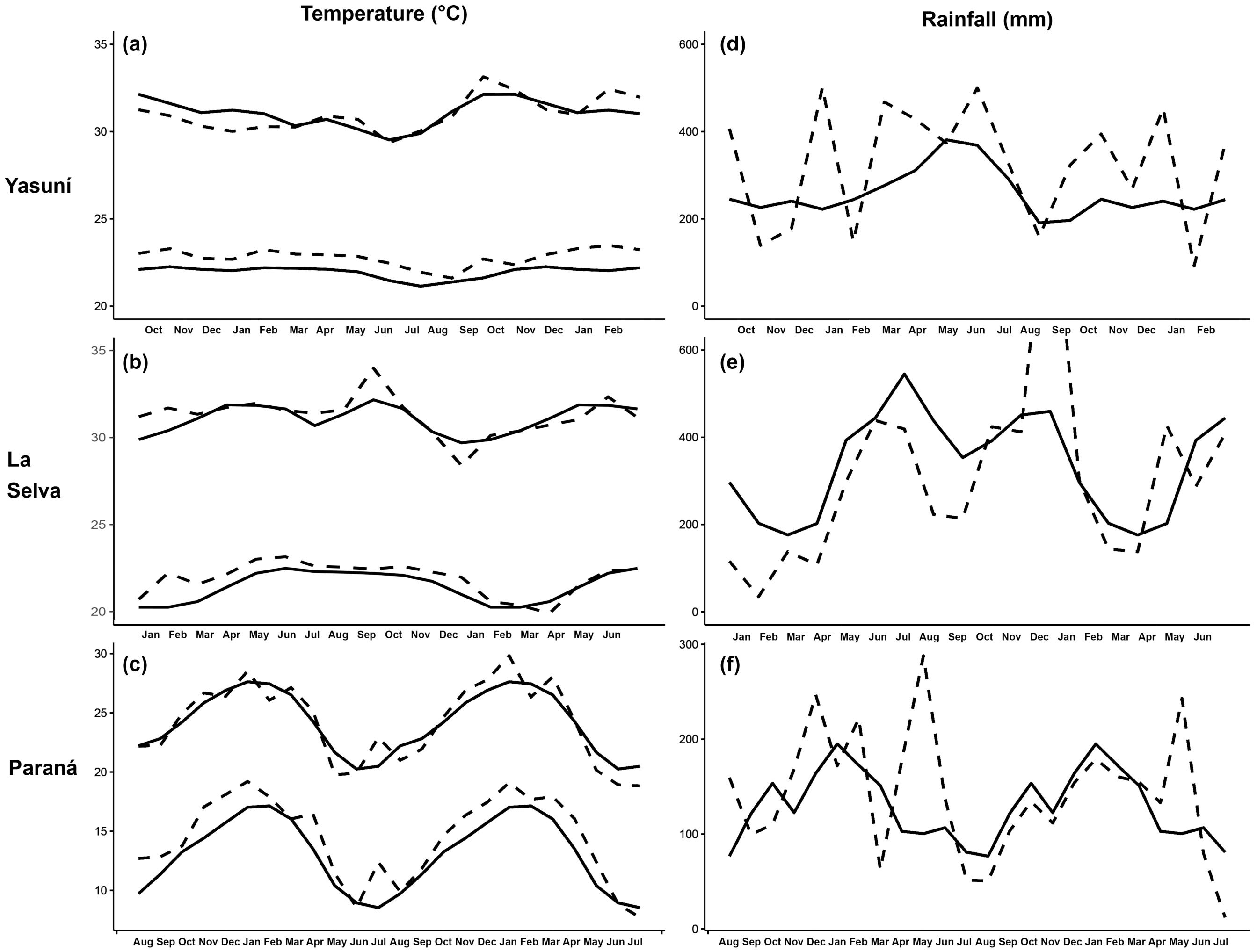

FIGURE 1 Comparative climate and weather data for Yasuní, Ecuador; La Selva Biological Station, Costa Rica; and the state of Paraná, Brazil. Left panels (a, b, c) are average daily temperature minima and maxima, by month. Right panels (d, e, f) are monthly rainfall. Solid lines are decadal-scale averages from the site (Yasuní, La Selva) or WorldClim averages (Paraná). Dashed lines are observed weather during the period of the study. For Paraná, the lines are the means of the eight sites.

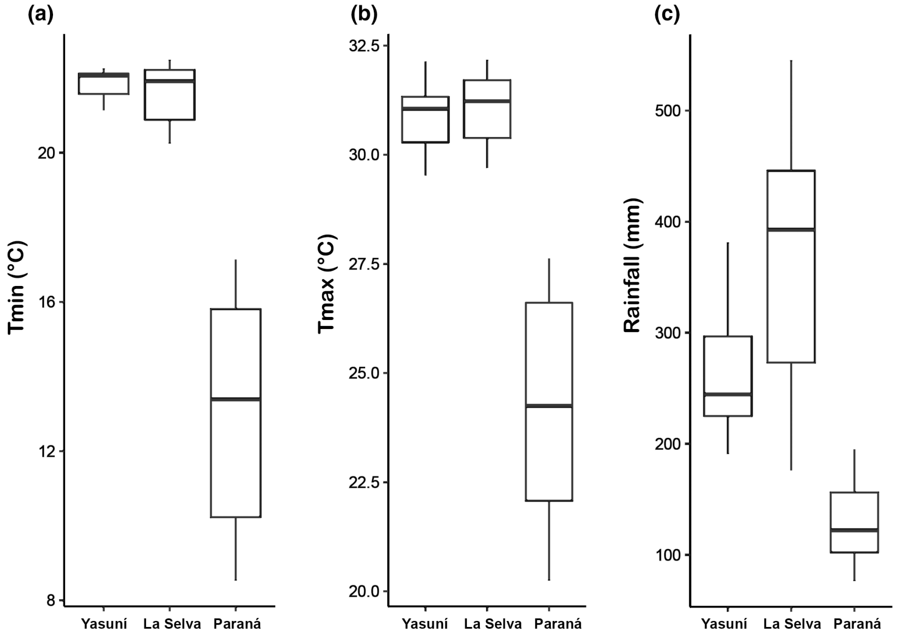

FIGURE 2 Contrasting seasonality among sites, based on long-term climate averages. Boxplots are based on the 12 monthly averages for (a) daily minimum temperature (Tmin), (b) daily maximum temperature (Tmax), and (c) monthly rainfall. Boxplots show median, 25th and 75th quartile (hinges), and whiskers (smallest or largest values no further than 1.5 × interquartile range from hinge).

TABLE 1 Flight seasonality statistics for army ant males at three neotropical sites

	La Selva, Year 1				Yasuní, Year 1			
	n	Mean	Rho	Rayleigh	*n*	Mean	Rho	Rayleigh
Cheliomyrmex andicola					5	11-Apr	0.7928	0.034
Eciton burchellii	4	16-Mar	0.9829	0.009	5	11-May	0.4981	n.s.
Eciton hamatum	3	29-Mar	0.6765	n.s.				
Eciton lucanoides	5	12-Apr	0.9983	0.001				
Eciton setigaster					1	31-Jul		n.s.
Labidus auropubens					1	3-May		n.s.
Labidus coecus	25	16-Jan	0.3482	0.047	12	25-Apr	0.2304	n.s.
Labidus mars denticulatus					6	17-Jan	0.7301	0.033
Labidus praedator s.s.					5	11-Oct	0.9189	0.007
Labidus p. sedulus					8	20-Aug	0.4152	n. s.
Neivamyrmex clavifemur					1	5-Feb		n.s.
Neivamyrmex digititipus	1	27-Sep						
Neivamyrmex fumosus	9	31-May	0.9557	<0.001				
Neivamyrmex gibbatus	1	26-May						
Neivamyrmex guyanensis					2	5-Mar	0.05234	n.s.
Neivamyrmex halidaii	8	13-Apr	0.8485	0.001	7	20-Apr	0.8625	0.002
Neivamyrmex klugii	17	5-May	0.9294	<0.001	1	2-Apr		n.s.
Neivamyrmex pilosus	10	30-Apr	0.975	<0.001				
Neivamyrmex radoszkowskii					2	21-Mar	0.7254	n.s.
Neivamyrmex rosenbergi								
Neivamyrmex spatulatus	3	29-Nov	0.9816	0.040				
Neivamyrmex spoliator	8	24-Apr	0.9379	<0.001				
Neivamyrmex swainsonii	7	12-May	0.9921	<0.001	2	23-Oct	0.9636	n.s.
Neivamyrmex walkerii					3	13-Apr	0.8097	n.s.
Nomamyrmex esenbeckii	15	25-Mar	0.9395	<0.001	5	4-Jun	0.4459	n.s.
Nomamyrmex hartigii	1	10-May						
	Paraná, Year 1				**Paraná, Year 2**			
	n	**Mean**	**Rho**	**Rayleigh**	***n***	**Mean**	**Rho**	**Rayleigh**
Eciton burchellii	19	18-Nov	0.8263	<0.001	11	16-Nov	0.2692	n.s.
Eciton quadriglume	20	11-Apr	0.9692	<0.001	24	17-Apr	0.968	<0.001
Eciton vagans	12	15-Jan	0.9689	<0.001	12	5-Jan	0.95	<0.001
Labidus coecus	66	1-Oct	0.7482	<0.001	48	8-Sep	0.6552	<0.001
Labidus mars	17	10-Sep	0.9561	<0.001	13	31-Aug	0.9064	<0.001
Labidus praedator	52	21-Mar	0.5011	<0.001	42	4-May	0.5269	<0.001
Neivamyrmex carinifrons	2	27-May	1	n.s.	4	22-Apr	0.9793	0.01
Neivamyrmex clavifemur	5	15-Feb	0.9763	0.002	5	11-Feb	0.9841	0.002
Neivamyrmex detectus	42	12-Feb	0.8681	<0.001	42	20 Feb	0.8078	<0.001
Neivamyrmex halidaii	21	14-Nov	0.9612	<0.001	13	17-Nov	0.9556	<0.001
Neivamyrmex hetschkoi	7	9-Apr	0.9338	<0.001	7	7-Apr	0.9389	<0.001
Neivamyrmex hopei	5	8-Nov	0.9735	0.002	4	23-Nov	0.9793	0.01
Neivamyrmex iheringi	15	13-Mar	0.9337	<0.001	28	7-Feb	0.8239	<0.001
Neivamyrmex jerrmanni	58	30-Mar	0.8464	<0.001	47	9-Apr	0.8473	<0.001
Neivamyrmex klugii	9	25-Nov	0.944	<0.001	1	15-Nov		n.s.
Neivamyrmex latiscapus	10	19-Nov	0.9805	<0.001	2	15-Nov	0.9994	n.s.

TABLE 1 (Continued)

	Paraná, Year 1				Paraná, Year 2			
	n	Mean	Rho	Rayleigh	*n*	Mean	Rho	Rayleigh
Neivamyrmex piraticus	22	26-Jan	0.9235	<0.001	12	3-Feb	0.9693	<0.001
Neivamyrmex punctaticeps	7	29-Nov	0.9489	<0.001	3	25-Nov	0.9676	0.045
Neivamyrmex sulcatus	5	6-Mar	0.8857	0.011	4	2-Mar	0.9681	0.012
Neivamyrmex swainsonii	1	27-Oct		0.512	0			
Nomamyrmex esenbeckii	24	23-Oct	0.943	<0.001	10	1-Oct	0.9656	<0.001
Nomamyrmex hartigii	72	18-Oct	0.8851	<0.001	42	16-Oct	0.8991	<0.001

Note: Sample sizes (*n*) are the number of trap nights in which a species occurred. The mean date of occurrence is based on circular statistics. Rho is a measure of dispersion, with values 0 for evenly dispersed through the year to 1 for perfectly clustered occurrences. The Rayleigh test is for significant difference from a random distribution of occurrence dates, with *p* values shown in the table.

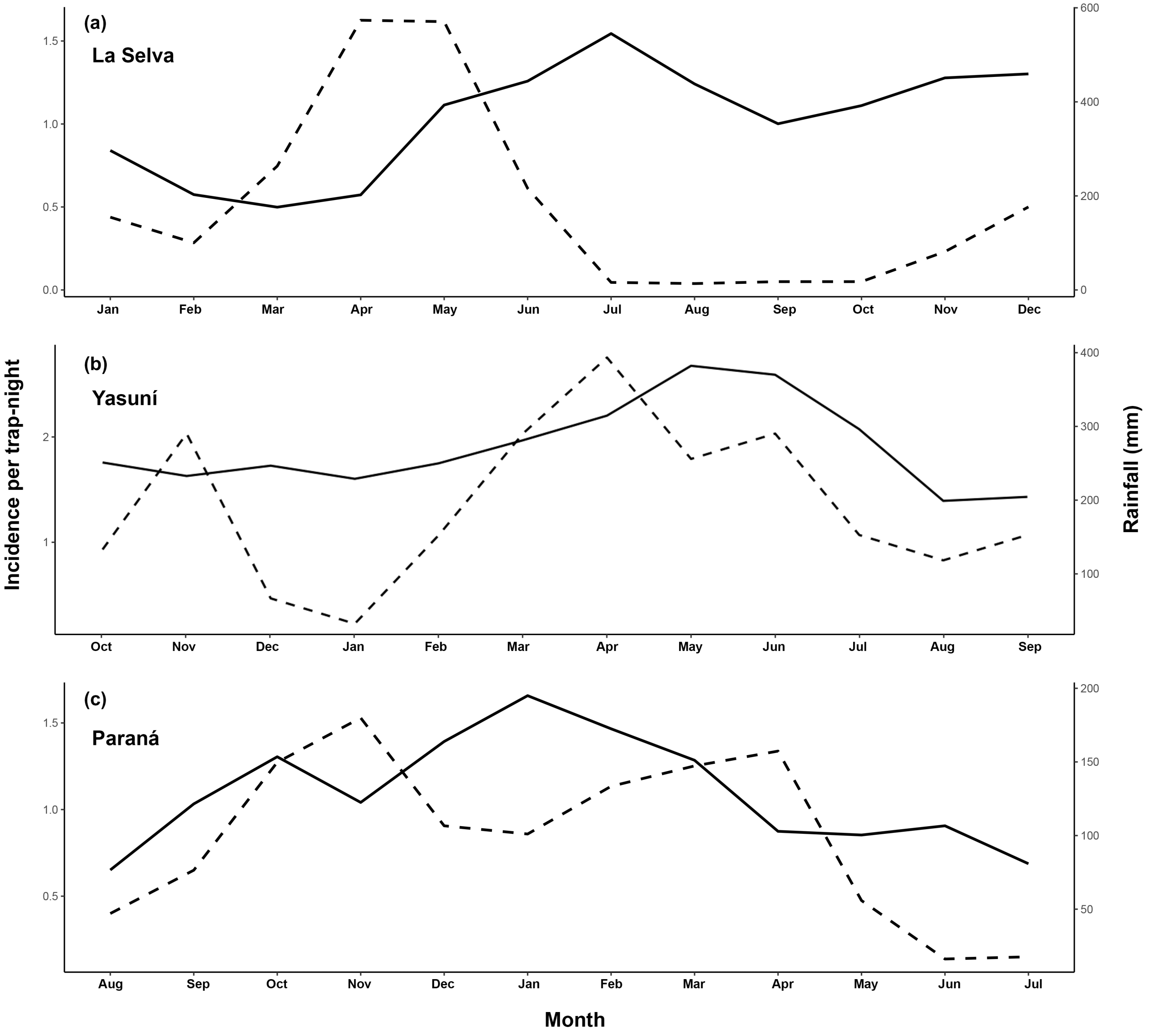

FIGURE 3 Overall male army ant flight activity and rainfall at (a) La Selva Biological Station, Costa Rica; (b) Yasuní, Ecuador; and (c) Paraná, Brazil. Dotted lines are the average summed incidence per trap night (= average number of species per trap night). Solid lines are long-term averages of monthly rainfall.

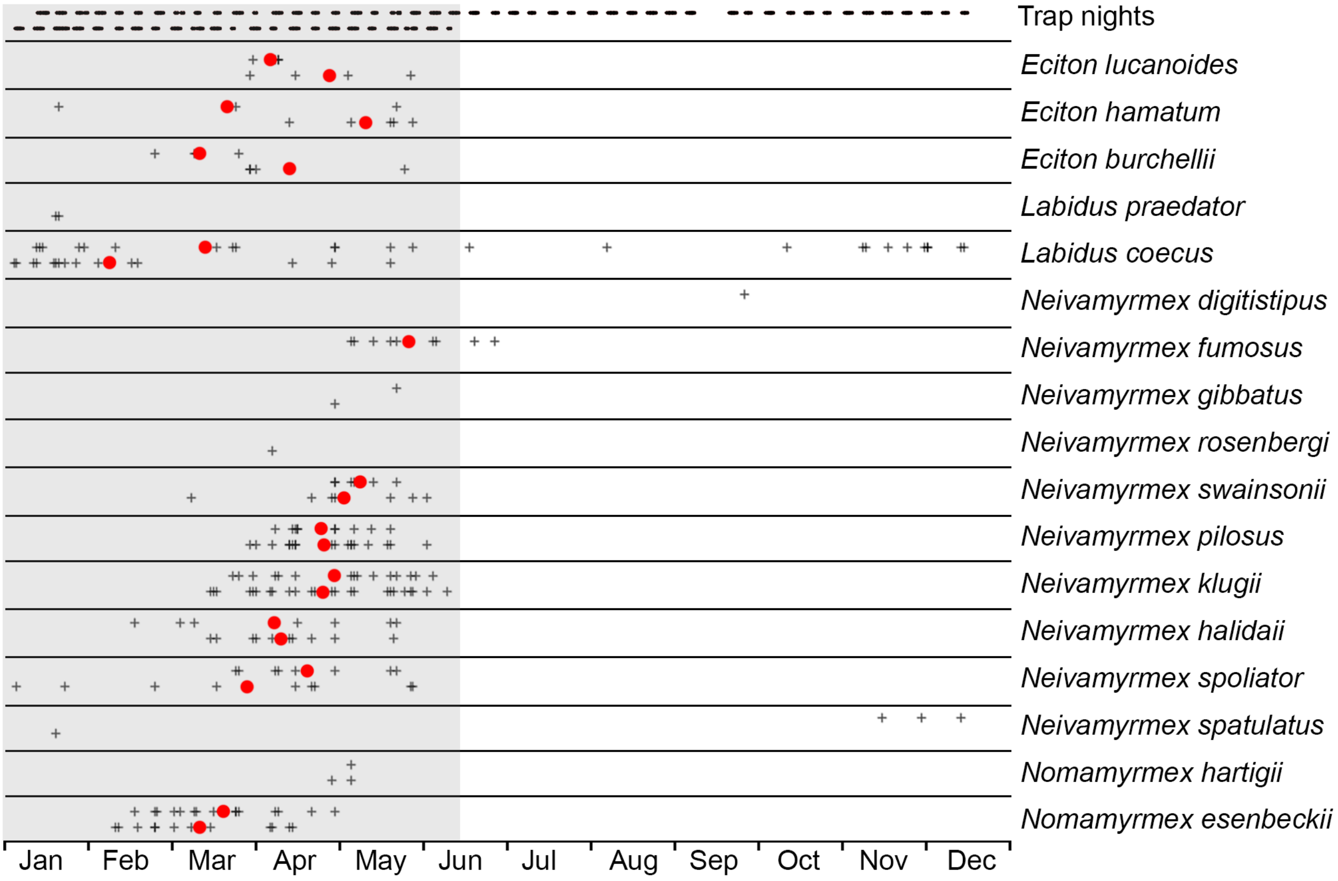

FIGURE 4 Male army ant flight activity at La Selva Biological Station, Costa Rica. Sampling was for 18 months, from January 1998 to June 1999. The horizontal axis is the date, but truncated such that after 12 months the occurrence data "wrap" onto a second row. The shaded portion of the graph is the overlap (the portion of the year that was sampled in both 1998 and 1999). Plotting the overlap in this fashion shows interannual variability in occurrence. The top row shows trap nights. Each "+" marker is occurrence of a species in one or both traps placed on a given night (i.e., canopy and ground traps). Species are grouped by genus and roughly in order of seasonal appearance within genera. Red dots are means for the overlapping portions of the two years. Means are not shown for species with low sample size.

anomalous in appearing abundantly during the first year of sampling, in late dry season, yet not appearing at the same time the following year. Other species generally show predictable reappearances at the same times in the two years. *Neivamyrmex spatulatus* is exceptional in appearing during the late wet season.

Yasuní was the least seasonal of the sites, although there is a rainfall peak from April to June. Most species had occurrences spread throughout the sampling period (Figure 5). Four species had significant Rayleigh tests. *Cheliomyrmex andicola* and *Neivamyrmex halidaii* had significant clustering (*rho* values 0.79 and 0.86, $p < .04$ and .002, respectively) with means in April, during the rainfall peak. *Labidus mars denticulatus* and *L. praedator s.s.* had significant clustering (*rho* values 0.73 and 0.92, $p < .03$ and .007, respectively) with means in January and October.

4 | DISCUSSION

In the tropical and subtropical Americas, local assemblages of 20 or more army ant species occur, and their presence and abundance can be assessed by the adult males that must occasionally fly from one nest to another. We measured male army ant flight activity at three Neotropical sites. Our studies revealed rich variation in army ant male behavior. Species varied in how high they fly, whether they fly during the day or at night, and whether they fly in early evening or predawn. Most showed strong intraspecific synchrony, with mean flight dates that were species-specific, yet clustered in particular periods of the year. An exception was the genus *Labidus*, which mostly lacked strong seasonality. The sites differed greatly in temperature and rainfall seasonality. Sites in Costa Rica and Ecuador had minimal seasonal variation in temperature, but did vary in rainfall. Although both are rainforest sites with average rainfall above 200 mm in every month, both experience relative wet and dry seasons. In each case, overall army ant male activity peaked during the transition from dry season to wet season, a pattern similar results in Panama (Donoso et al., 2022; Kannowski, 1969). In the Brazilian state of Paraná, a subtropical region with cold dry winters and warm wet summers, army ants generally flew in the warm months, but with peak activity in early and late summer, and a dip in activity during midsummer. These aggregate patterns emerged from the individual phenologies of multiple species. However,

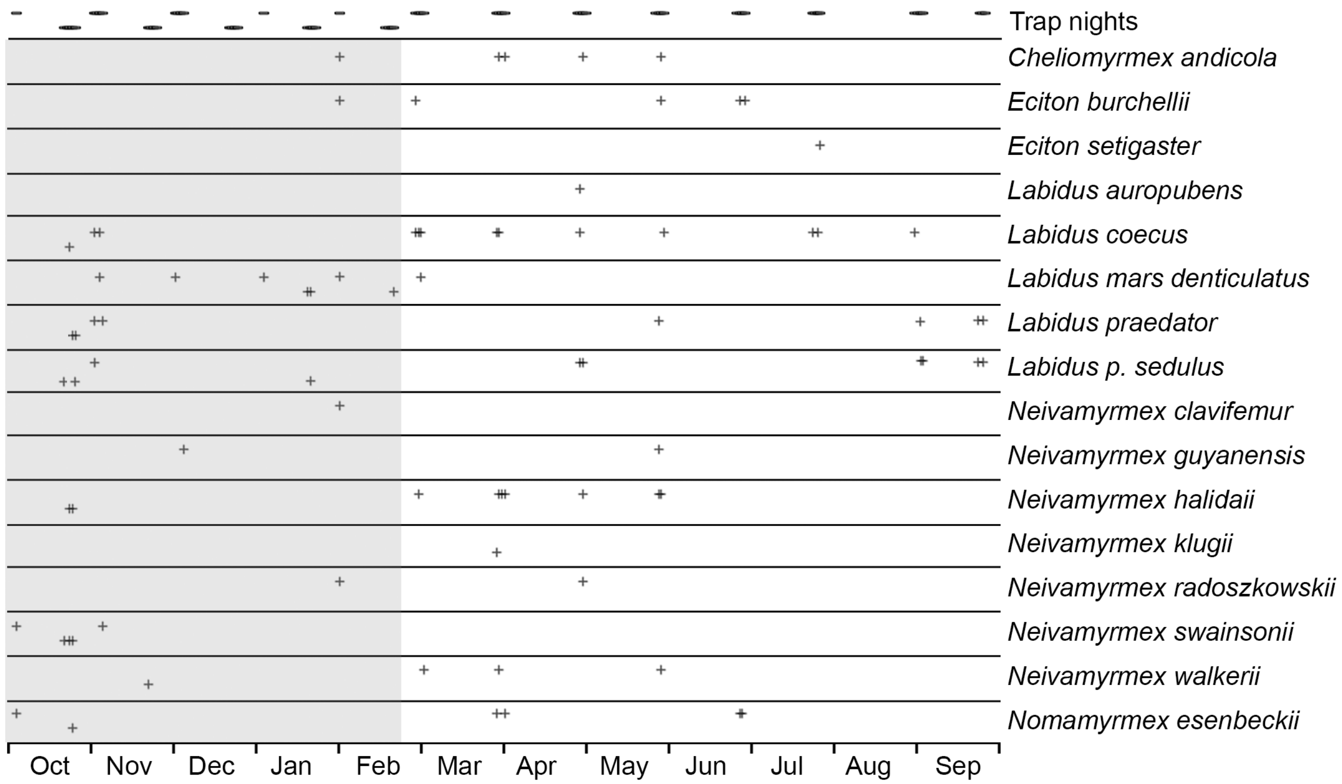

FIGURE 5 Male army ant flight activity at Yasuní, Ecuador. Sampling was for 17 months, from October 2018 to February 2020. The horizontal axis is the date, truncated to 12 months, and the occurrence data are wrapped as in Figure 4. The shaded area is the portion of the year that was sampled in sequential years, showing interannual variability in occurrence. The top row shows trap nights. Each "+" marker is occurrence of a species in a trap. Species are in alphabetical order.

phenologies varied dramatically among species and among sites. At the sites in Costa Rica and Paraná, individual species tended to be highly synchronized and seasonal themselves, in addition to yielding the aggregate signal. In contrast, many species at the Ecuadorian site, near the equator, showed little or no flight synchrony, and the aggregate seasonality emerged from the weak or undetectable seasonality of individual species. Here we discuss factors that may influence both the timing and the degree of synchrony of flight activity, considering both ultimate and proximate causes. When insects show seasonality, an important distinction is made between ultimate causes, such as availability of food or mates, and proximate causes, the cues such as day length, temperature, or rainfall that trigger growth or reproduction.

Reproduction at seasonal transitions may be related to food availability (Donoso et al., 2013). During non-reproductive brood cycles, army ants are replenishing their worker force with each cycle. During reproductive cycles, workers are not produced (Schneirla & Brown, 1952), presumably resulting in an extended period when colony size decreases as a result of worker loss. This is compounded by colony fission following mating, resulting in abrupt decreases in colony size. It may be essential during these periods of small worker number for per capita worker food capture to be high. Thus there may be selection for colony reproduction to occur during periods of maximum prey availability. Seasonal transitions may be associated with increased arthropod abundance (Kaspari, Pickering, Longino, & Windsor, 2001; Levings & Windsor, 1996). How can army ant colonies synchronize reproduction during these favorable seasons?

Army ants have what may be considered an extreme form of female-calling behavior (Kaspari, Pickering, Longino, & Windsor, 2001). Female-calling ant species in the tropics typically have broad reproductive periods and prolonged male flight seasons (Helms, 2018; Shik et al., 2013). Thus one might expect a prolonged flight season in army ants, with individual colonies having synchronized sexual brood production, but asynchrony among colonies such that males and virgin queens would be available throughout the year. Instead, we observe a high degree of reproductive synchrony both within and among army ant species. Given the reproductive biology of army ants, there is no option of gradually producing sexuals and retaining them in the nest until an appropriate environmental cue (Gotwald, 1995). The decision to make a reproductive brood, and thus the cue, must occur at least a month before the optimal time for reproduction. Although rain-associated food availability may determine the optimal time, it cannot be the cue.

A second function of mating synchrony, independent of food resources, is increasing local mate density (Calabrese & Fagan, 2004). The evolution of synchronized mating activity of whole populations may be favored by sexual selection processes involving mate location and mate choice. Lower bounds to population density may be set by the ability to find mates, an Allee effect. Synchronous mating may allow populations to persist at lower densities.

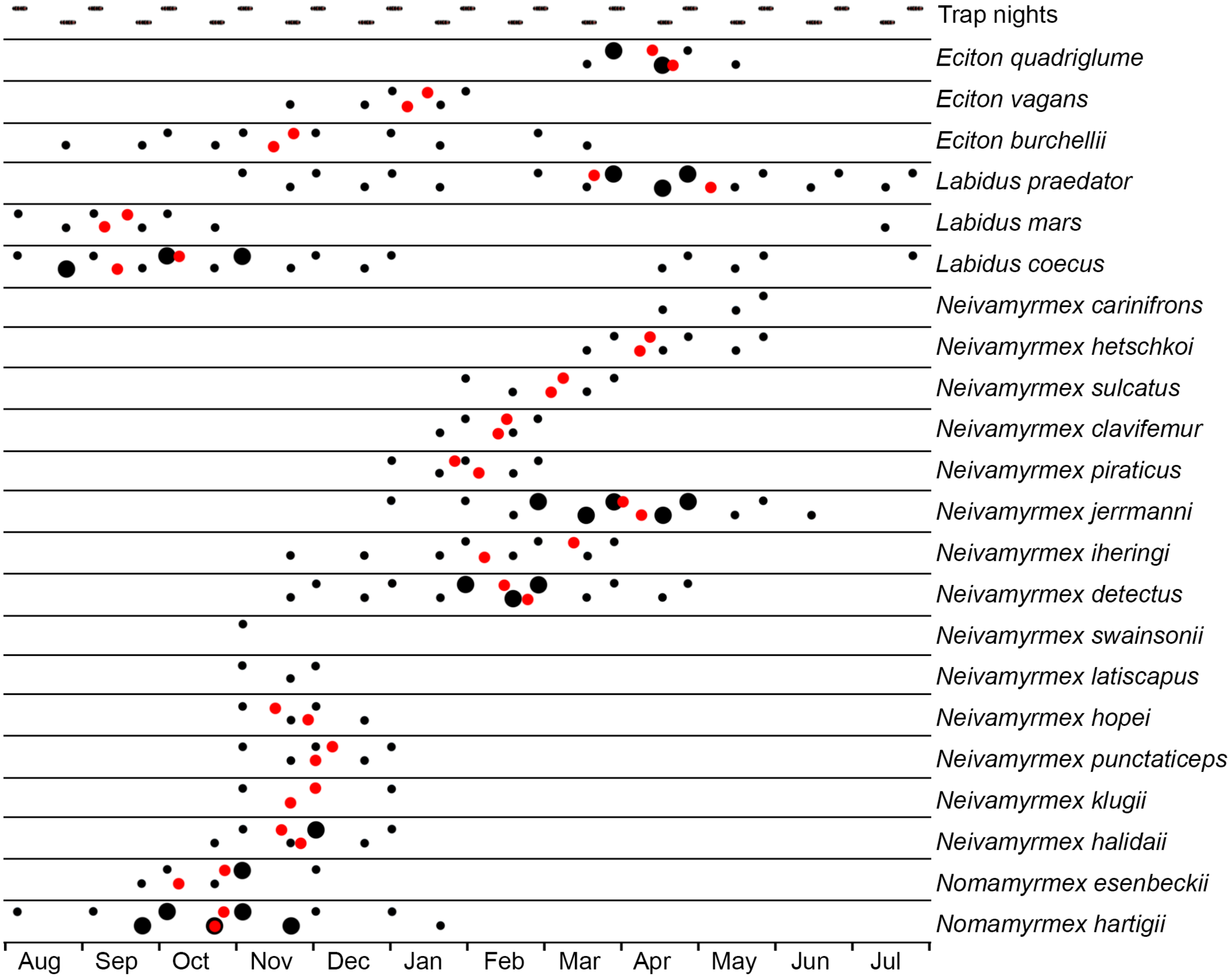

FIGURE 6 Male army ant flight activity in the state of Paraná, Brazil. Sampling was for 24 months, from august 1986 to July 1988. The horizontal axis is the date, truncated to 12 months, and the occurrence data are wrapped, as in Figures 4 and 5, to show interannual variability. The top row shows trap nights. Each dot represents occurrence in at least one trap night during a 5-night trapping session across 8 sites (potential incidence values 1–40). Small dots are incidence values 1–10; large dots are >10. Species are grouped by genus and roughly in order of seasonal appearance within genera. Red dots are means. Means are not shown for species with low sample size.

Mating synchrony typically requires environmental cues, and in most regions of Earth such cues are abundantly available (Frederickson, 2006; Kaspari, Pickering, & Windsor, 2001). At distance from the equator, day length is an absolutely reliable cue. Insects can differentiate day length changes as little as half an hour, and critical day lengths have been observed for some insects at latitudes as low as 7°. However, within 5° of the equator the signaling capacity of seasonal change in day length appears to be lost (Denlinger, 1986). Temperature becomes both an increasing constraint and an increasingly reliable cue with increasing latitude (Dean & Dean, 2018). Rainfall can be highly seasonal and its availability can be a major constraint, shaping the optimal timing of reproduction, but year to year variation may make it an unreliable cue.

In the highly seasonal environments at the latitudinal limits of army ants, most or all species show strong seasonality. In Texas and Arizona in the United States, males fly in summer (Baldridge et al., 1980). In our study, the Paraná species mostly show strong seasonality, flying during the warm, wet summer. Baldridge et al. (1980) found variable and minor effects of short-term weather (rain, humidity, temperature changes) and lunar phase on male flight activity, and likewise we see no evidence of conspicuous male flight response to sudden rainfall or other short-term effects. As observed by Baldridge et al. (1980), we also observed that flight times of different species were staggered through the season. In the Paraná data, the species were also highly predictable from one year to the next. This implies that some reliable cue is being used to trigger simultaneous sexual brood production by multiple colonies of a species. Given the interannual variability in rainfall, rainfall is unlikely to be the cue. In Paraná, temperature and day length are highly correlated, and either is a potential cue.

At La Selva Biological Station, at just 10°N latitude, annual day length and temperature variation are small, yet most species also

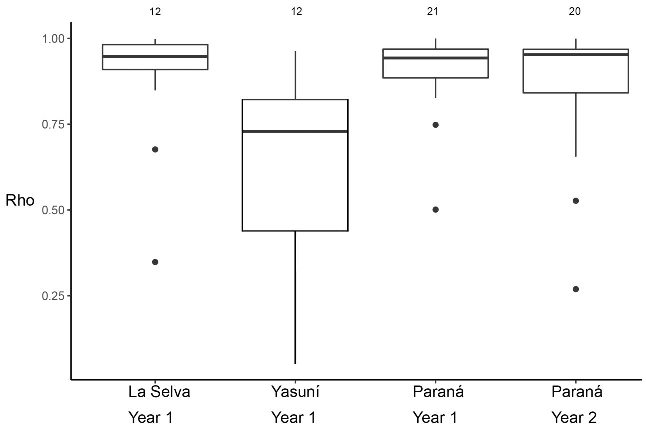

FIGURE 7 Distribution of *rho* values for flight dates of army ant males, year 1 at La Selva Biological Station, Costa Rica; year 1 at Yasuní, Ecuador; and the two separate years in Paraná. In circular statistics, *rho* is a measure of dispersion varying from 0 (uniform) to 1 (perfectly synchronized). Replicates are species with at least two occurrences. Box plots show median, hinges, whiskers, and outliers. Sample sizes are above boxes. *Rho* values were significantly different among sites (1-way ANOVA, $p < .001$).

show strong seasonality in flight times, concentrated in the dry season and especially during the transition to wet season, similar to results from nearby Panama (Donoso et al., 2022; Kannowski, 1969). Yet given the high interannual variability in rainfall and low interannual variability in flight times, perhaps day length is still a sufficient cue to synchronize reproductive activity (Denlinger, 1986). Wolda (1989) similarly proposed day length as the emergence cue for cicada species on Barro Colorado Island in Panama. Nascimento et al. (2011) found high levels of army ant flight seasonality for Ilheus, Brazil, a site at 14°37″S. They found a correlation of flight with temperature and not rainfall, suggesting temperature as the seasonal cue. However, they only analyzed climate variables, and day length varies by more than an hour at that latitude and thus could also be a reliable cue.

Yasuní, Ecuador, exhibits negligible annual variation in temperature or day length, and relatively minor seasonality in rainfall. In these conditions, army ant males appear to lose much or all seasonal synchrony. Loss of synchrony may have conservation implications, if higher local densities are required to ensure at least a few colonies are producing sexuals at any time. In the narrow band of weakly seasonal Amazonian rainforest along the equator, higher population sizes or densities may be required to prevent local extinction. There is no evidence that current population densities correlate with degree of seasonality (i.e., Yasuní does not have higher density than La Selva or BCI; O'Donnell et al., 2007). But these are all sites with relatively intact habitat and healthy army ant communities, and other factors may determine density. The effect of seasonality on lower population limits would best be tested in habitat fragments at the edge of army ant sustainability.

The genus *Labidus* stands out as an exception, with phenology distinct from other army ants. *Labidus* species typically have broader flight seasons or weaker seasonality in general, and, for *L. coecus* in particular, the time of peak flight is different from most other species. In Texas, *Labidus coecus* flew in early Spring, while all other species flew later (Baldridge et al., 1980). At La Selva, *L. coecus* had the weakest seasonality, and peak flight period was mid wet season rather than dry season. In Ilheus, *L. coecus* flew during the coldest time of year, while all other species flew in the warmer part of the year (Nascimento et al., 2011). The results were the same in a study of three *Labidus* species in Minas Gerais, Brazil (Nascimento et al., 2004) and in our data set from Paraná. *Labidus coecus* flew during the coldest months, while other species flew in the warmer months. In addition, in Paraná, both *L. coecus* and *L. praedator* had much weaker seasonality and broader flight times than all other species. *Labidus coecus*, in particular, seems almost universally "off season" compared to other army ants.

Among army ants, the genus *Labidus* is exceptional in multiple characteristics. *Labidus* species have the most generalized diet among all army ants. Both *L. coecus* and *L. praedator* prey on ants and other arthropods, but they may also forage on plant material (Borgmeier, 1955; Rettenmeyer, 1963) and there are observations of *L. coecus* preying on river turtle nests (da Costa Reis et al., 2021). Another distinction is that *Labidus* species appear variable in the degree of brood synchrony. Both synchronous and asynchronous broods have been observed in *L. coecus* and *L. praedator* (Fowler, 1979; Powell & Baker, 2008; Rettenmeyer, 1963). *Labidus coecus* is distinctive in other ways, inhabiting a broader range of habitats than almost any other ant. It occurs nearly everywhere in the New World tropics and subtropics, from Texas to Argentina, from sea level to over 3000 m elevation, and in almost any habitat type (Wetterer & Snelling, 2015). *Labidus coecus* is often among the most abundant army ants in local assemblages (Kaspari & O'Donnell, 2003; O'Donnell et al., 2007). Foraging is almost entirely subterranean, unlike its congener *L. praedator* (Rettenmeyer, 1963). Despite occupying a great range of habitats and climates, *L. coecus* actually has a narrower thermal tolerance than many other army ants, perhaps due to its largely subterranean habits (Baudier et al., 2018). If thermal tolerance parameters are similar between workers and males, males of highly subterranean species may be more sensitive to heat and desiccation, favoring flights during cooler, wetter periods. Perhaps the combination of broader diet, high abundance, subterranean habits, and lack of brood synchrony all interact somehow to shift peak flight times compared to other species, and to reduce the need for reproductive seasonality.

For species that show flight synchrony, there appears to be a degree of species specificity in flight date. Staggered flight times might suggest some structuring due to competitive exclusion or reproductive isolation. Males have highly species-specific genitalia, which must function as a female choice mechanism at the moment of copulation, once males are in the nest. But the signals that flying males use to locate nests are completely unknown. If there were species-specific odor cues, there would be no need for temporal segregation. However, if males used more generalized "army ant" odors or visual cues of nocturnal foraging trails, temporal segregation could be selectively advantageous. A male entering a nest of a different species might successfully reach the queen but be rejected due to genitalic mismatch, and subsequently be killed by the workers. It may also be that phylogenetically related species will share attraction cues, necessitating temporal segregation among close relatives but not from more distantly related species. More species-level phylogenies of Neotropical army ants are needed to investigate the degree of conservatism vs. divergence of flight date. Alternatively, even if males use highly species-specific attraction signals, with no sexual selection for temporal segregation, there will still be selection for a degree of synchrony simply to find mates. There may be selection for optimal flight date to occur during a favorable season, but with staggered flight dates due to stochastic variation. Local optimal flight time variation could also be caused by gene flow, with each species having a flight time that reflects optimal conditions integrated over the geographic range. There is no evidence of over-dispersed flight times among species, as also noted by Baldridge et al. (1980). Selection may favor narrow flight times within species, but there may be no interactions among species and specific mean flight times may be somewhat stochastically distributed within a broad envelope of suitable times.

A subset of army ant species can be easily monitored using light traps. More long-term sampling programs would improve our understanding of army ant male phenology and the long-term stability of their assemblages. More extensive spatial sampling could reveal how landscape features shape army ant assemblages and survival. Our phenology results suggest when to concentrate sampling efforts to achieve greater geographic coverage. We encourage renewed and continued monitoring of these keystone predators.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.00000006s (Tozetto et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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