ORIGINAL ARTICLE

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The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction

Abstract Reproductive phenologies reflect the interaction between the mating system of a taxon and the local environment. Ant colonies reproduce and disperse via the flights of winged alates. Few data exist on the reproductive phenologies of ant assemblages. Here we analyze the reproductive phenologies of 81 common ant species from 23,182 individuals collected over 3 years on Barro Colorado Island, Panama (BCI). Species ranged from highly synchronous to continuous fliers, but showed a median flight duration of at least 8 of 13 lunar months. In two statistical analyses (variance ratio test and Spearman rank correlations), 84% (16 of 19) of ant genera had species trending toward positively associated phenologies, more than expected by chance ($P<0.00036$ by a binomial test). Thus, there was little evidence for the hypothesis that competition for limiting resources staggers congeneric flights and ultimately promotes reproductive isolation. On the contrary, the timing of reproduction, and its synchrony, tended to be conserved within genera and subfamilies. These results closely match phenological studies of plant assemblages. The continuous reproduction and small colony size of many species in this study suggest that the female calling syndrome, a poorly documented mating system in ants, may be common on BCI.

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Introduction

A key component of an organism's life history is the timing of reproduction and dispersal. Most ant colonies, like most plants, are sessile perennials that allocate resources to growth, maintenance, and reproduction on an annual schedule (Rathcke and Lacey 1985; Andersen 1991; Keller and Genoud 1997). Species within an ant assemblage often differ in their diel and seasonal foraging activity (Whitford 1978; Lynch et al. 1980; Cerda et al. 1997; Kaspari and Weiser 2000). Far less is known, however, about the phenology of ant reproduction and dispersal (Tschinkel 1991) even though this knowledge is key to understanding patterns of genetic and species diversity. It is an especially intriguing topic for tropical assemblages where over 100 species may be found in 100 m² of forest (M. Kaspari and J.T. Longino, personal observation).

Here we present the first data set documenting patterns and possible mechanisms generating phenological diversity in a tropical ant assemblage. We begin by briefly exploring the major constraints to the reproductive phenology of an ant population. We then discuss how taxonomic diversity in phenologies may arise.

What determines the reproductive phenology of an ant population?

Reproductive and dispersal phenologies are compromises to a variety of biotic and abiotic constraints (Rathcke and Lacey 1985). In ants, a key element of this constraint is the dual nature of the flights themselves: alates must not only find a mate, but females must then go on to found a colony.

Ants show at least two mating systems that involve alates (Hölldobler and Bartz 1985). Both have a pheno-

logical signature. In male aggregation, males gather in large numbers at microsites that are often reused yearly, sometimes marking these sites with pheromones (Wilson 1957; Brian 1979; Hölldobler and Bartz 1985). Females join these aggregations, mate, and fly off to found a colony, after which the males die. Perhaps due to the need to attain a critical mass of males, male aggregation flights tend to be highly synchronized, with mating swarms occurring at the same time each year. In female calling, individual females use pheromones to advertise for searching males (Janzen 1967; Hölldobler and Bartz 1985), a syndrome also found in solitary wasps (Haskins 1978). In contrast to male aggregation, the phenologies of species showing the female calling syndrome "do not appear to be well synchronized at the level of either the colony or population of colonies" (Hölldobler and Wilson 1990). The female calling syndrome has been identified in at least four ant subfamilies (Janzen 1967; Kannowski and Johnson 1969; Hölldobler 1971; Hölldobler and Haskins 1977). However, it is less often documented than male aggregation, perhaps due to the often spectacular apparency of the latter (summarized in Hölldobler and Wilson 1990). Passive traps that can capture even inconspicuous, asynchronous flights are ideally suited to detecting the signatures of these two mating systems.

Two abiotic factors – temperature and rainfall – further constrain the timing of reproductive flights. The length of the flight season tends to increase toward the equator (Kaspari et al. 2001), suggesting temperature limitation. Alate flights are often linked to recent rains (Morrill 1974; Hölldobler 1976; Hölldobler and Wilson 1990; Diehl-Fleig 1993) that may serve to (1) cue synchronous flights, (2) soften soil for nest excavation, (3) minimize desiccation, and (4) act as a cue to the start of the productive season. On Barro Colorado Island (BCI), a seasonal Panama rainforest, high weekly rainfall was necessary but not sufficient to produce flights in one-third of the common ant species (Kaspari et al. 2001).

What determines the reproductive phenology
of a taxocene?

Taxocenes are ecological assemblages of phylogenetically related species. Ant taxocenes would be expected, due to phylogenetic constraints and/or adaptations to similar environments, to fly on similar schedules (McCluskey 1992). We know of no statistical tests of this proposition for ants.

However, if congeneric species rely on different resources (e.g., host plants) or conditions (e.g., activity temperatures) that vary in time, alate flights may be staggered. This would be evolutionarily significant, as these ecological differences would be linked to a process that simultaneously limits hybridization (Hölldobler and Wilson 1990; Futuyma 1998). Two plant taxocenes – Neotropical *Heliconia* (Stiles 1977; Poole and Rathcke 1979; Cole 1981) and Paleotropical *Shorea* (Ashton et al. 1988) stagger flowering times, perhaps in response to selection to decrease competition for pollinators.

Taxa that show temporal staggering of flight phenologies mostly do so over a 24-h time scale. These include *Myrmica* in a temperate bog (Kannowski 1959), *Pogonomyrmex* in a temperate desert (Hölldobler 1976), and *Dorylus* (Haddow et al. 1966) and three ecitonine genera (Kannowski 1969) in tropical rainforests. In contrast, there has been little systematic search for the staggering of flights on an annual time scale. One possible case, (the army ant genus *Neivamyrmex*: Baldridge et al. 1980; Hölldobler and Wilson 1990) has not been statistically analyzed and combines records of 16 species over all of North America.

Lowland tropical rainforests, with hundreds of ant species and a year-round warm climate, provide an ideal environment for the staggering of flight times on an annual time scale. Here we analyze the behavior of 19 genera (81 species), testing for (1) staggered flight phenologies among closely related species and (2) the phenological signatures of two common mating systems.

Methods

Data in this study came from two sets of traps on BCI (9°9′19″ N, 79°50′15″ W), a lowland, seasonally wet forest in Lake Gatun of the Panama Canal. Rainfall on BCI averages about 2,500 mm annually, with a distinct dry season during the first third of the year. See Leigh et al. (1996) for further site description.

Ants were sampled with black lights and malaise traps. Two modified Pennsylvania black-light traps (henceforth light traps) were suspended from the forest canopy on a ridge top (120 m) in old-growth forest. They hung 3 and 27 m from the forest floor. Light traps capture night-flying insects. Traps were run continuously, and harvested weekly for 1 year beginning mid June 1991. Ants were separated out of the catch and preserved in 70% ethanol. For further description of the black-light studies on BCI see Wolda (1992). Two Townes-style Malaise traps were placed in an old-growth forest ravine, separated by 65 m, in mid June 1992. Unlike light traps, Malaise traps are passive and do not attract insects, capturing both the day- and night-flying fauna. Malaise traps were harvested weekly and the catch was stored in 70% ethanol. We analyzed alate activity from the first 2 years of these samples. For both light and Malaise trap samples, we examined flight phenology by pooling weekly captures of both traps into 13, 4-week lunar months.

Specimens were identified to species and morphospecies through the use of keys, matching specimens to material at the Museum of Comparative Zoology, Harvard, and through taxonomic consultations. Our ability to identify alates to species varied across taxa. Keys are available for alates of only a few genera; species series in museums often lack associated alates. Females of all species were identified to genus and, when possible, identified to species. Male morphology in the ants, in contrast, is often highly conserved. Male specimens were first identified to subfamily (the one exception are many males of the subfamilies Dolichoderinae and Formicinae which cannot be readily distinguished). They were then sorted to genus, when possible, and to species/morphospecies, relying heavily on matching males to those from the Harvard collection. The collections reside at the University of Oklahoma. Taxonomy conforms to Bolton (1995), including the recent revision of the Dacetonini (Bolton 1999).

We compiled data on 81 taxa represented by at least 20 individuals. Plots of flight duration versus sample size began to stabilize at this number. The 81 species varied over two orders of mag-
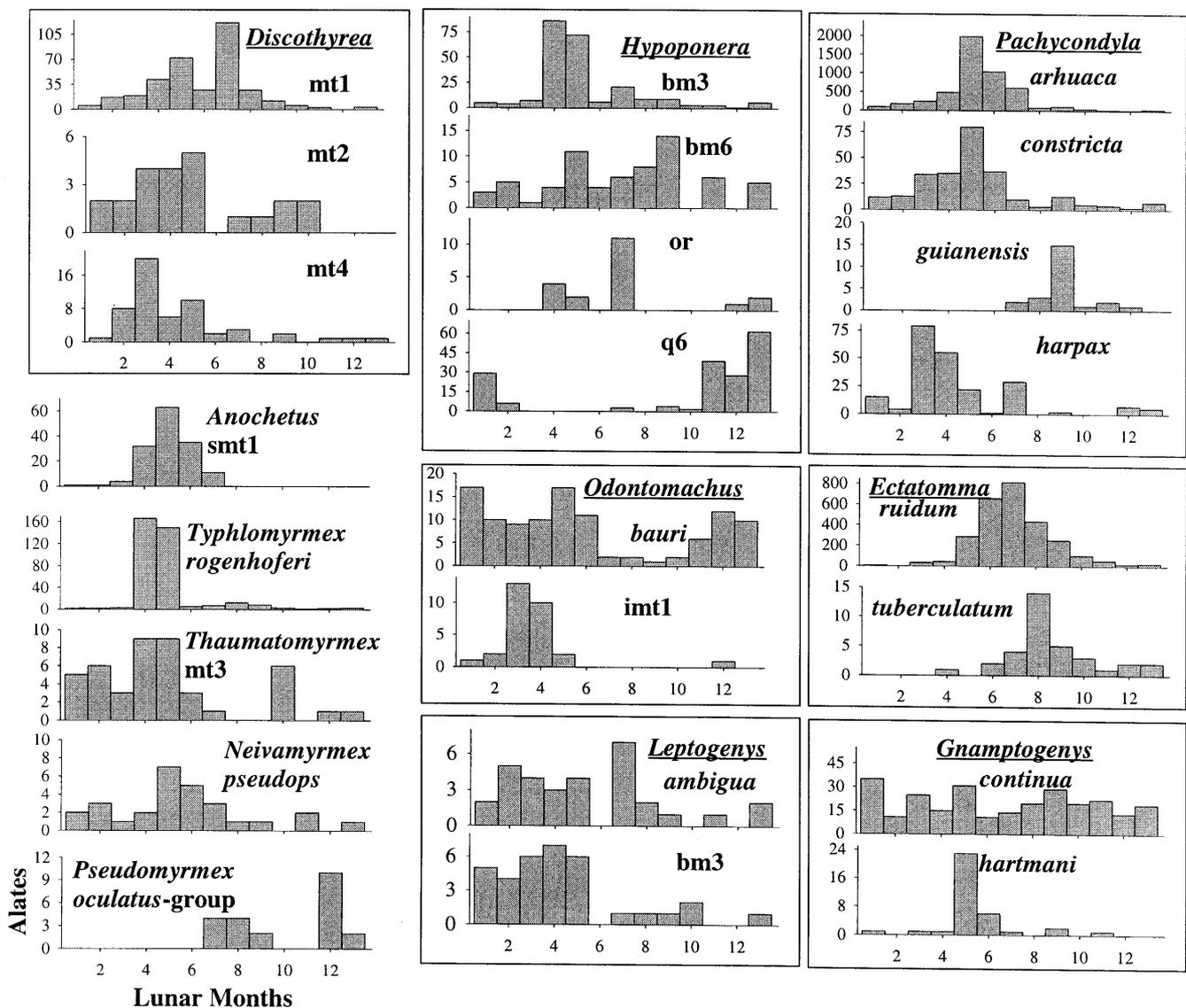
Fig. 1 Phenologies of common species from the subfamily Poner-inae on Barro Colorado Island, plus one Ecitoninae (*Ne-ivamyrmex*) and one Pseudomyrmecinae (*Pseudomyrmex oculatus* group). Phenologies are the pooled activity from two Malaise traps and two light traps. Lunar months are 4 weeks long. Conge-nerics are *boxed*

nitude in number of individuals sampled (minimum=20, maxi-mum=4922, median=67).

We examined patterns of synchrony, measured as a species' coef-ficient of variation in activity (the ratio of the standard deviation in flight activity over 13 months to the mean across those months). Synchrony was unrelated to the number of individuals sampled (Pearson's $r=-0.12$, $P=0.2559$). Long flight duration (in months) and low values of synchrony would suggest the continuous flights of the female calling syndrome; the converse would suggest the highly pulsed flights of the male aggregation syndrome. We used ANOVAs to test for significant heterogeneity in synchrony at the genus level (using species values) and subfamily (using genus means).

Most species in our data set tend to fly most of the year, vary greatly in abundance, and often show multiple modes (see Figs. 1, 2, and 3). The variance ratio test (Schluter 1984) was thus most ap-propriate to gauge the tendency of congeners to stagger versus clump their phenologies across the 13 lunar months (Gotelli and

Graves 1996; N. Gotelli, personal communication). As species with-in a genus could vary by two orders of magnitude in abundance, and the variance ratio test is sensitive to extremes, we transformed the abundance data into percent abundance per month per species. To avoid false-positive associations, we used only the months in which at least one member of the taxon was flying. As monthly counts of flight activity for a species were unlikely to be statistically indepen-dent, we did not test for significant deviation from the null ($V=1$, random association) for each genus. Rather, we used a binomial test to evaluate the hypothesis that more genera showed staggered phe-nologies (Vs<1) than would be expected by chance.

As a check on the variance ratio test, we also calculated the mean Spearman rank correlation for all possible pairs of species in each genus. We evaluated the null hypothesis of equal numbers of positive and negative correlations using a binomial test.

Results

The 81 species showed a diversity of phenologies (Figs. 1, 2, and 3). Flight duration varied from 13 months (e.g., the ponerine *Pachycondyla constricta*; Fig. 1) to 3 months (e.g., the formicine *Camponotus cur-*
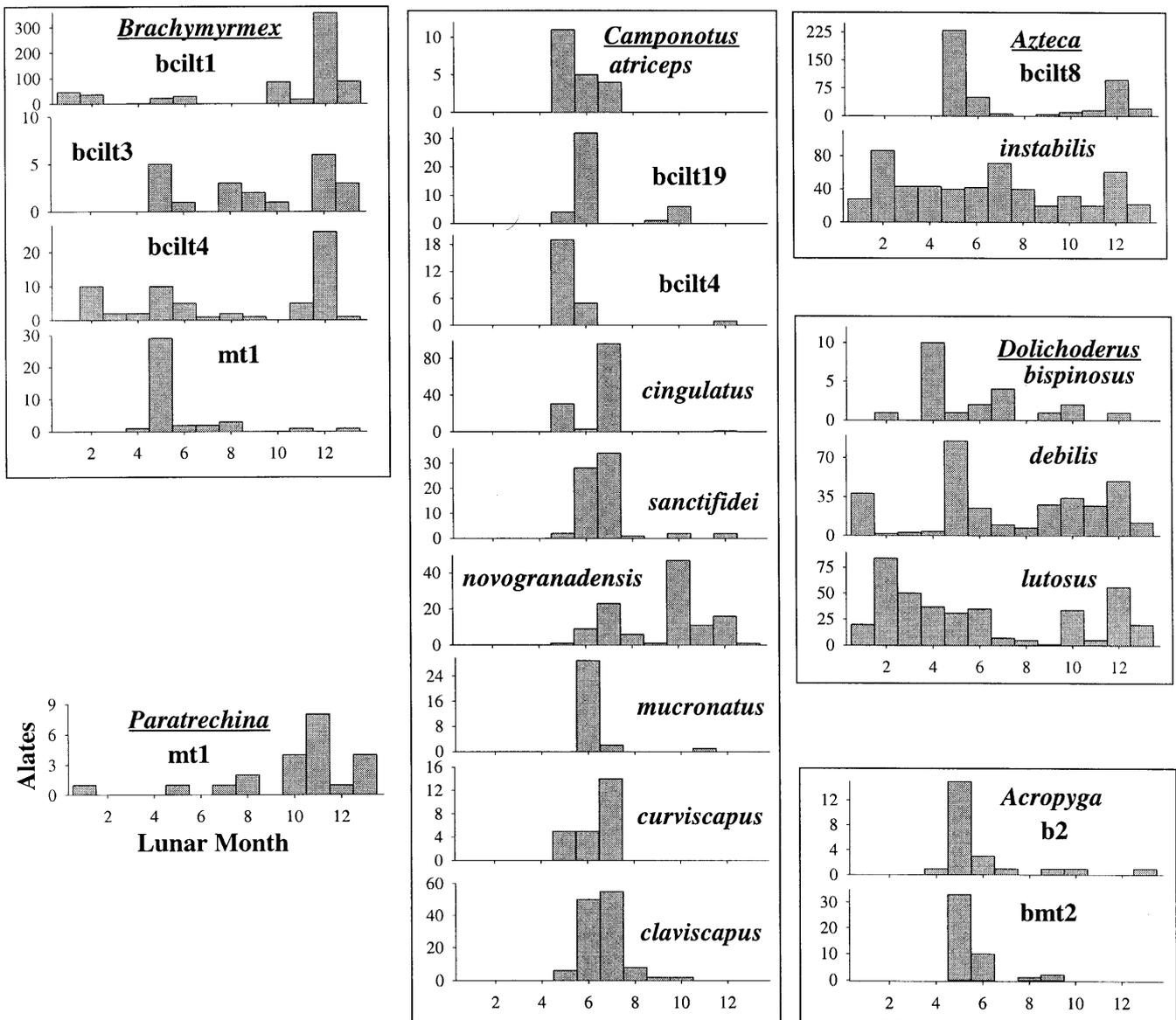
Fig. 2 Phenologies of common species from the subfamily Dolichoderinae (*Azteca* and *Dolichoderus*) and Formicinae (all else). Phenologies are the pooled activity from two Malaise traps and two light traps. Lunar months are 4 weeks long. Congenerics are *boxed*

viscapus; Fig. 2) with a median and mode of 8 lunar months. However, given that sample size was correlated to duration (Pearson's r=0.35, P=0.0012), many species likely flew more months than were recorded. The lunar month in which a species showed its peak flight activity also varied considerably among the 81 species, with at least one species peaking in activity each month (Fig. 4). However, over one-third of the species studied showed peak activity in lunar month 5 (at the transition from the dry to the wet season).

Flight synchrony, measured as a coefficient of variation of activity, varied from 38 (e.g., the continuously flying ponerine *Gnamptogenys continua*; Fig. 1) to 341

(the highly pulsed myrmicine *Trachymyrmex* mt1; Fig. 3a) with a median of 166. Synchrony tended to have a phylogenetic component. Genera from three of the four subfamilies show a broad range of coefficients of variation of flight activity (Fig. 5). Genus membership accounted marginally (P<0.0513) for variation in synchrony ($F_{18,49}$=1.81, mean-square model=6,600, mean-square error=3,645) for 19 genera represented by at least 2 species in our data set. Synchrony differed among subfamilies (P<0.0369, $F_{3,26}$=3.28, mean-square model=9,427, mean-square error=2,878) using four subfamilies each with at least 2 genera (for a total of 30 genera). Mean synchrony for the ponerine and dolichoderine genera tended to be 20–30% smaller than those of the myrmicine and formicine genera (Fig. 5).

The variance ratio test statistic V ranged from 3.71 (*Camponotus*) to 0.73 (*Myrmicocrypta*; Table 1). The majority of genera evaluated (16 of 19, 84%) yielded V>1.0, more than predicted if positive and negative asso-
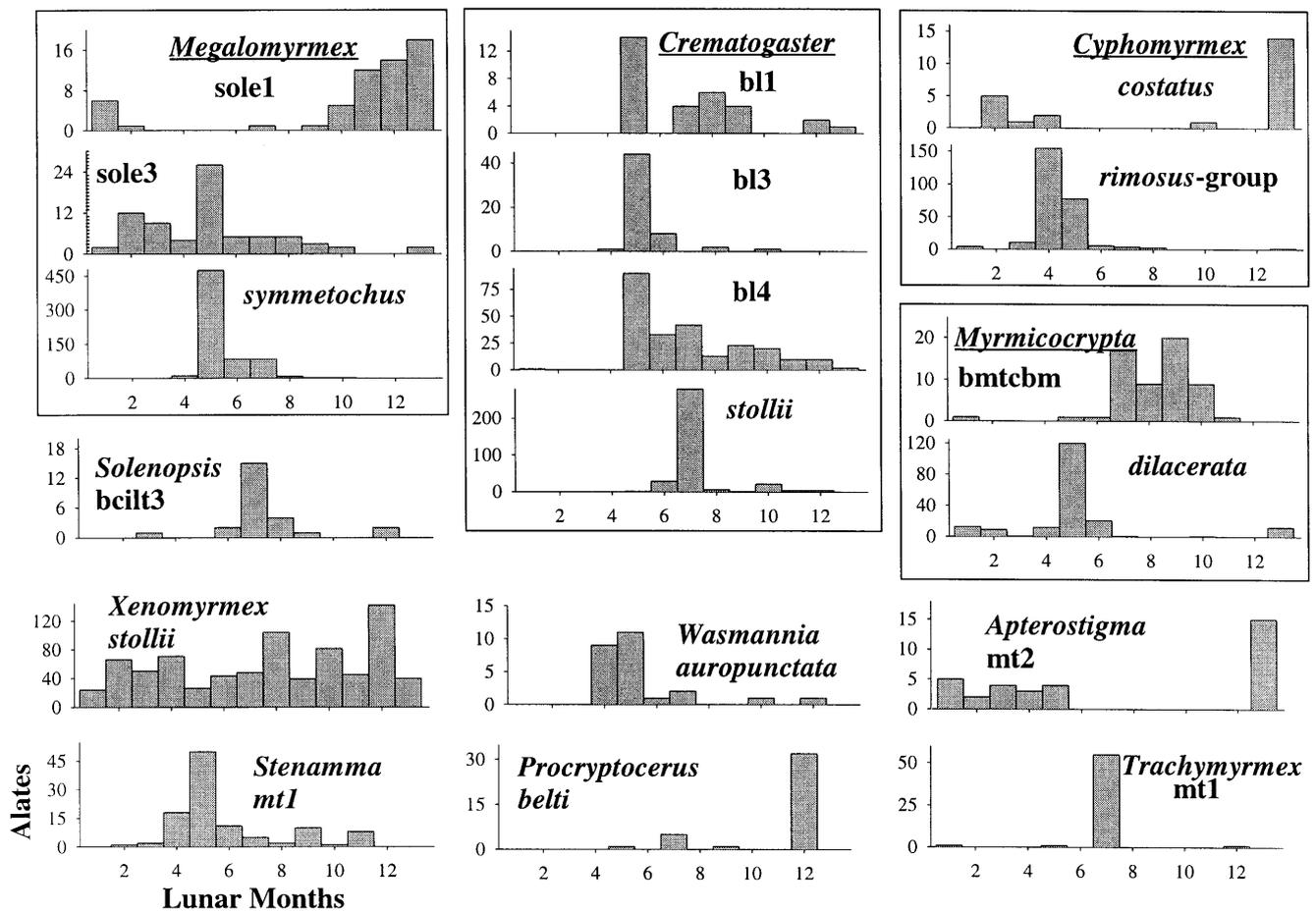
a

Fig. 3a,b Phenologies of common species from the subfamily Myrmicinae. Note that the one or more of the three morphospecies of *Strumigenys* may belong to *Pyramica*, based on Bolton's (1999) revision. Phenologies are the pooled activity from two Malaise traps and two light traps. Lunar months are 4 weeks long. Congenerics are *boxed*

Table 1 Patterns of annual phenologies for 19 ant genera with two or more species represented by at least 20 individuals. Two metrics of association are presented, the variance ratio test V and the Spearman rank correlation r_s calculated as the average of all possible species pairs. $V<1$ and $r_s<0$ suggest a trend toward the staggering of phenologies

Subfamily	Genus	Number of species	Number of months	V	r_s
Formicinae	*Camponotus*	9	9	3.71	0.554
Myrmicinae	*Strumigenys*	6	13	3.20	0.363
Myrmicinae	*Pheidole*	10	13	2.17	0.312
Formicinae	*Acropyga*	2	8	1.98	0.565
Myrmicinae	*Pyramica*	2	12	1.97	0.672
Formicinae	*Brachymyrmex*	4	13	1.94	0.153
Myrmicinae	*Crematogaster*	4	11	1.88	0.449
Ponerinae	*Discothyrea*	3	13	1.73	0.547
Ponerinae	*Ectatomma*	2	12	1.4	0.592
Ponerinae	*Leptogenys*	2	11	1.29	0.602
Ponerinae	*Hypoponera*	4	13	1.28	0.143
Myrmicinae	*Megalomyrmex*	3	13	1.16	−0.334
Ponerinae	*Odontomachus*	2	13	1.13	0.510
Ponerinae	*Gnamptogenys*	2	13	1.12	0.365
Ponerinae	*Pachycondyla*	4	13	1.09	0.061
Dolichoderinae	*Azteca*	2	13	1.01	−0.222
Myrmicinae	*Cyphomyrmex*	2	10	0.87	0.003
Dolichoderinae	*Dolichoderus*	3	13	0.85	0.008
Myrmicinae	*Myrmicocrypta*	2	12	0.73	−0.282

Fig. 3b (continued)

b
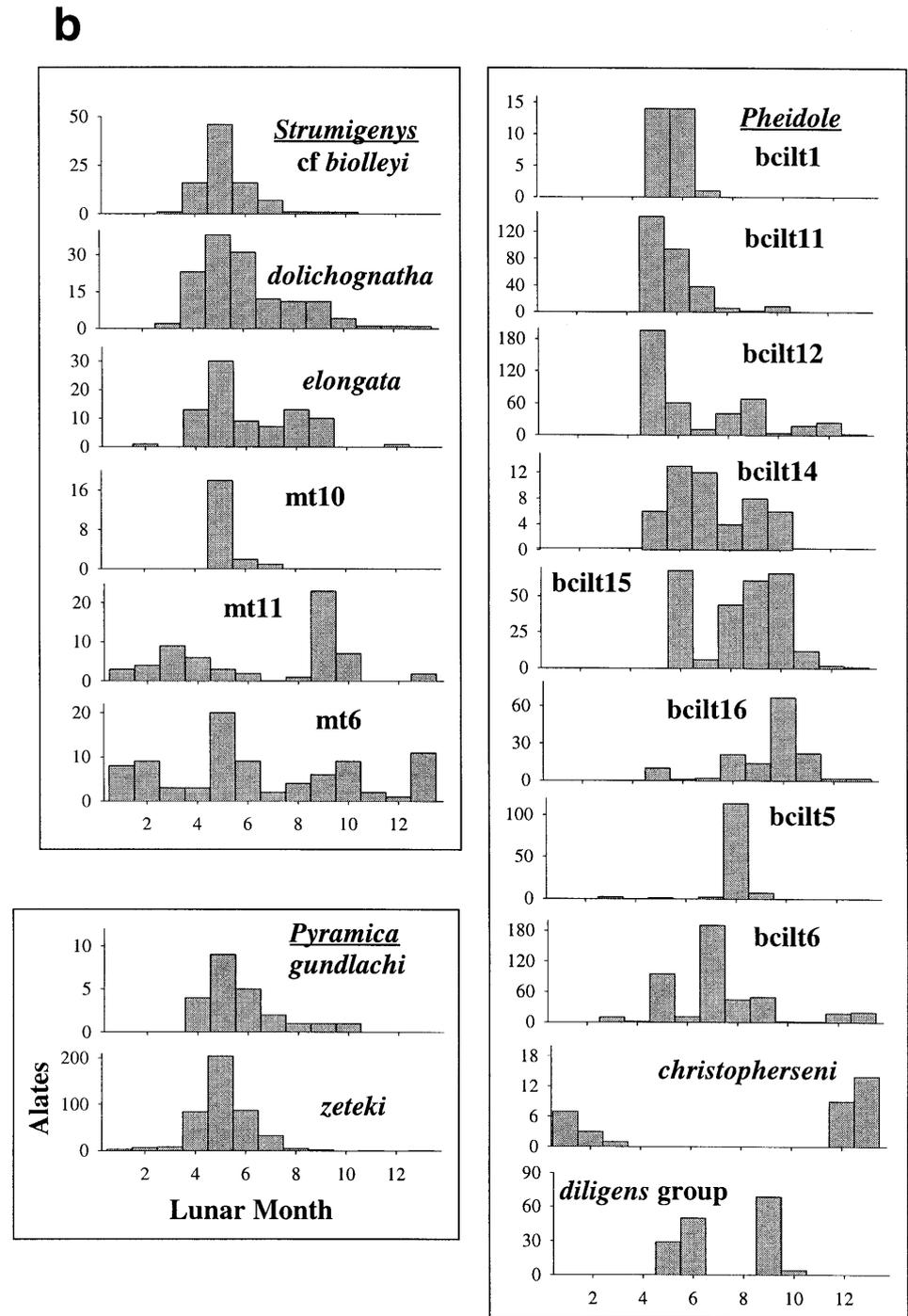
ciations were equally likely ($P<0.00037$ by a binomial test). We obtained similar results when calculating the mean Spearman rank correlations for all possible species pairs of a genus (Table 1). Mean r_s ranged from 0.672 (*Pyramica*) to –0.334 (*Megalomyrmex*), and the majority of genera tested (16 of 19, 84%) showed a positive r_s, more than predicted by chance ($P<0.00037$ by a binomial test). In total, five genera are suggested by at least one of the two tests to stagger flights. This still constitutes fewer than expected by chance (14 of 19, 74%, $P<0.0096$). Thus, there is little evidence for a wide-

spread staggering of flight times among congeners on BCI. Instead, these data suggest that members of the same genus tend to fly at the same time.

Discussion

The flight phenology of an ant population links in time two key aspects of its life history – sexual reproduction and colony foundation. The everwarm tropical environment provides a long, temporal niche axis upon which to

stagger this activity (Kaspari et al. 2001). Eighty-one species from BCI show a diversity of phenologies, from nearly continuous flight activity (e.g., *Xenomyrmex stollii*; Fig. 3a) to strong pulses in different months of the wet season (e.g., *Megalomyrmex symmetochus*, *Pheidole* bcilt5; Fig. 3a, b). However, while there is ample opportunity for temporal segregation, there is little evidence of it – the median flight duration in this assemblage is at least 8 months, and more genera tend toward *positive* associations in flight phenology than staggered phenologies. This is the first study we know of to examine the phenology of a tropical assemblage, and the first that does not rely on directly observing alate flights (e.g., Talbot 1965).

The ants on BCI thus appear to have relatively conserved reproductive phenologies, a pattern also shown for two plant taxocenes (Kochmer and Handel 1986;
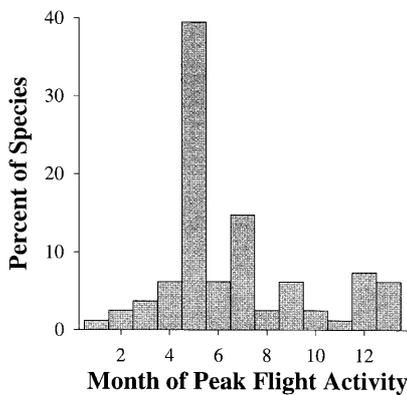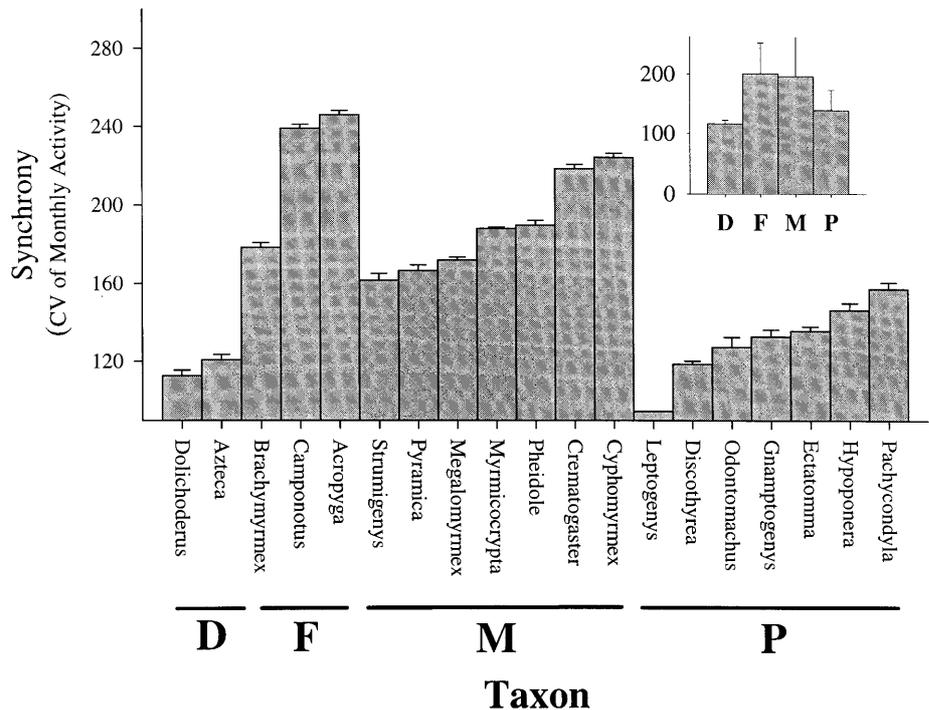

Fig. 4 Distribution of peak month of flight activity for 81 species from Barro Colorado Island, Panama

Wright and Calderon 1995). Such similarity can occur for many reasons (Schluter 1984). One hypothesis is that flight phenologies are phylogenetically constrained. A second, and not mutually exclusive, hypothesis is that conditions good for one species are good for other, closely related species. The onset of the wet season (lunar months 5–8) offers foundresses the likely benefits of deep litter and thick vegetation, a more benign microclimate, and higher food supplies (Cornejo et al. 1994; Levings and Windsor 1996). Most species on BCI show peak flight activity in this period (Fig. 4). Finally, the pulse of rain at the onset of the wet season may be one of the few, unambiguous cues available on BCI. Even if there is a benefit to segregating flight times, the lack of predictable cues throughout the year may prevent such asynchrony.

While these data suggest that species, especially in the most diverse genera on BCI, lack systematic differences in their phenologies, many species on BCI have phenologies that are clear "outliers" compared to their congeners (e.g., *Pheidole christopherseni*, *Strumigenys* "mt11", *Camponotus novogranadensis*). The life histories of these species may tell us much about the factors that constrain alate phenologies. Furthermore, our rejection of staggered phenologies on an annual timescale does not address the hypothesis that BCI genera stagger reproduction over 24 h. We are currently looking into this possibility.

Many species on BCI (particularly from the Formicinae and Myrmicinae) have the high coefficient of variation of flight activity symptomatic of the male aggregation syndrome. At least two of the genera with pulsed reproduction (*Acropyga* and *Cyphomyrmex*) have been observed in mating swarms (Weber 1972; J.T. Longino,

Fig. 5 Synchrony of alate flights (±1 SD) as measured by the coefficient of variation in flight activity (i.e., high CV=highly synchronous flights). *Larger graph* characterizes the synchrony distribution among common genera; the *smaller graph* represents mean values for the four common subfamilies (*D* Dolichoderinae, *F* Formicinae, *M* Myrmicinae, *P* Ponerinae)

personal observation). However, even these species, with highly synchronous reproduction, also "dribble" alates in off-peak months (e.g., *Acropyga* b2, Fig. 2). Flying in the off-peak could be costly if mating success is some positive function of aggregation size. However, the cost of asynchrony may be relaxed if the high population densities of many tropical species (Kaspari et al. 2000) enhance effective population size (Bawa 1977; Primack 1980).

In contrast, the low synchronies of many species (particularly from the Dolichoderinae and Ponerinae) are consistent with the female calling syndrome. A variety of evidence supports this hypothesis. The myrmicine *X. floridanus* exhibits female calling (Hölldobler 1971); on BCI its congener *X. stollii* has one of the most asynchronous flights (CV=55; Fig. 3a). Small colony size, another characteristic of the syndrome (Hölldobler and Wilson 1990) is a common syndrome in tropical species (Kaspari and Vargo 1995). Finally, at least three genera on BCI (*Ectatomma*, *Odontomachus*, and *Pachycondyla*) possess a gland that may produce female calling pheromone (Hölldobler and Haskins 1977). If female calling is common on BCI, it suggests that at any one time, searching males must distinguish among many pheromone plumes, given the 286 species we have collected thus far from our traps.

Other factors may favor continuous reproduction in the tropics. Species that occupy plant cavities in treefall gaps (e.g., some *Cecropia*-ants of the genus *Azteca*) may find nest sites rare but continuously renewing. Species that occupy multiple nests (polydomy) with multiple queens (polygyny) may have the opportunity to join extant colonies year-round. In short, the evidence for female calling – a poorly understood, and perhaps underdocumented mating system – on BCI is circumstantial and requires further investigation. A better understanding of the causes and consequences of these phenologies may further our understanding of both speciation and coexistence in this diverse assemblage.

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