

The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites

Megan E. Frederickson

Received: 23 November 2005 / Accepted: 4 May 2006 / Published online: 7 June 2006
© Springer-Verlag 2006

Abstract In saturated tropical ant assemblages, reproductive success depends on queens locating and competing for scarce nest sites. Little is known about how this process shapes the life histories of tropical ants. Here I investigate the relationship between nest site availability and an important life history trait, reproductive phenology, in the common Amazonian ant species *Allomerus octoarticulatus*. *A. octoarticulatus* is a plant-ant that nests in the hollow, swollen stem domatia on *Cordia nodosa*. I provide evidence that nest sites are limiting for *A. octoarticulatus*. Most queens produced by *A. octoarticulatus* colonies died before locating suitable host plants, and most queens that located hosts died before founding colonies, probably from intraspecific competition among queens for control of host plants. I further show that the reproductive phenology of *A. octoarticulatus* closely matches the seasonal availability of its nest sites, domatia-bearing *C. nodosa* saplings. Both the production and flight of *A. octoarticulatus* reproductives, and the number of *C. nodosa* saplings available for colonization by ants, peaked from March to May. There was correlative evidence that *A. octoarticulatus* colonies use temperature as a cue to synchronize their reproduction to the availability of *C. nodosa* saplings: both the production of reproductives by ant colonies and the number of *C. nodosa* saplings available for colonization were correlated with temperature, and not with rainfall. All of

these results suggest that nest site limitation constrains the reproductive phenology of *A. octoarticulatus*.

Keywords *Allomerus octoarticulatus* · Ant-plant · *Cordia nodosa* · Mutualism · Seasonality

Introduction

In tropical rainforests, ant colonies occupy most of the available space, and nest sites are probably a limiting resource for many ant species (Levings and Franks 1982; Hölldobler and Wilson 1990; Bourke and Franks 1995; Kaspari et al. 2000; Philpott and Foster 2005, but see Torres 1984). To found a new colony, a young ant queen must find, secure, and hold on to a nest site in the face of competition from other ants. Bourke and Franks (1995) suggest that patterns in the availability of nest sites in time and space should shape the life history of many ant species. However, there has been little empirical work showing how nest site limitation can influence the life history strategies of ants.

Obligate ant–myrmecophyte symbioses are excellent systems for the study of nest site limitation and life history in tropical ants. Myrmecophytes (ant-plants) are plants that have domatia—hollow, swollen stems, thorns, petioles, or leaf pouches in which ants nest (Heil and McKey 2003). Obligate plant-ants nest in domatia, usually on only one or a few species of myrmecophytes (Davidson et al. 1991). In many plant-ant species, foundress queens colonize host plants when the plants are saplings (Vasconcelos 1993; Yu and Pierce 1998; Frederickson 2005; Stanton et al. 2005). In these cases, a nesting opportunity is created when an ant-plant sapling produces its first domatia. This makes

Communicated by Judith Bronstein

M. E. Frederickson (✉)
Department of Biological Sciences, Stanford University,
Stanford, CA 94305, USA
e-mail: meganf@stanford.edu

ant-plant saplings easily identifiable, discrete resources that can be mapped and monitored over time.

Many plant-ant species are nest-site limited (Davidson et al. 1989; Vasconcelos 1993; Fonseca 1999; Stanton et al. 2002), suggesting that the temporal and spatial pattern of host plant availability may be important to plant-ants. Ant-plant populations are often saturated with ants (Fonseca 1999), and plant-ants often compete for hosts (Janzen 1973; Davidson et al. 1989; Fiala and Maschwitz 1990; Davidson and McKey 1993; Stanton et al. 2002, 2005). When nest sites are limiting, the reproductive success of an ant colony can be determined by the frequency with which foundress queens produced by the colony successfully locate, colonize, and compete for host plants.

The timing of reproduction can influence an organism's reproductive success. Reproductive phenologies often reflect species' adaptations to their abiotic and biotic environments (Rathcke and Lacey 1985; Kaspari et al. 2001b). In temperate ant species, reproductive timing is constrained by the need to mate, disperse, and found a colony before the arrival of winter (Kaspari et al. 2001b). By contrast, tropical ant species tend to have longer mating seasons, which can vary from highly synchronous to nearly continuous throughout the year (Kaspari et al. 2001a, b).

For tropical ants, one life history adaptation to nest site limitation may be to synchronize reproduction to the availability of nesting sites. Here I investigate this possibility in a common Amazonian ant species, *Allomerus octoarticulatus*, which nests in the ant-plant *Cordia nodosa*. I examine the relationship between its reproductive phenology and conditions favoring reproductive success. I describe the seasonal timing of alate production and flight for *A. octoarticulatus*, and estimate the mating flight success of queens by comparing the number of queens produced by colonies to the number arriving to found colonies. I also estimate the success of queens as they compete for nest sites and begin laying eggs. Finally, I investigate how temperature, rainfall, and nest site availability may influence reproductive phenology in *A. octoarticulatus*.

Materials and methods

Study site and climate data

This study was conducted at the Reserva Nacional Allpahuayo-Mishana (RNAM; 3°58'S, 73°25'W), near Iquitos in the Department of Loreto, Peru. The 58,000-ha reserve comprises a patchwork of vegetation types, including varillal forest on white sand soils and exten-

sive terra firme forest on clay soils. The forests of the reserve are among the most diverse in the world, with 275–289 tree species ha⁻¹ (Gentry 1988; Phillips et al. 1994).

The climate of the region is often considered aseasonal, because no month of the year receives less than 100 mm of rain (Sombroek 2001; Vieira et al. 2004). Total yearly rainfall ranges from 2,400 to 3,200 mm (Sombroek 2001). Rainfall is usually not distributed evenly throughout the year. Typically, March and April receive the most rain, while July, August, and September receive the least rain (Madigosky and Vatnick 2000). In most years, temperatures are coolest in June and July (Madigosky and Vatnick 2000).

Climate data for this study were collected from February 2004 to February 2005. Maximum and minimum temperatures were measured daily using a digital maximum/minimum thermometer. Rainfall was measured daily using a standard meteorological rain gauge.

Study system

Allomerus octoarticulatus demerarae Wheeler (Myrmicinae) is an obligate symbiont of the myrmecophyte *Cordia nodosa* Lam. (Boraginaceae). Both *A. octoarticulatus* and *C. nodosa* occur at high densities in the terra firme forests at RNAM. *A. octoarticulatus* seems to nest exclusively on *C. nodosa* (Yu and Pierce 1998; Yu et al. 2004). *C. nodosa* hosts several species of ants in addition to *A. octoarticulatus*, including *Azteca depilis* Emery (Dolichoderinae), *Myrmelachista schumanni* Emery (Formicinae), and two undescribed species in the genus *Azteca* (Frederickson 2005). Exploitative competition, but not direct interference competition, occurs among ant species for hosts (Yu et al. 2001). A single *C. nodosa* plant nearly always hosts only one ant colony (Yu et al. 2004; Frederickson 2005).

C. nodosa has hollow, swollen stem domatia in which ants nest. *C. nodosa* produces domatia whether or not ants are present. *C. nodosa* saplings start producing domatia when they reach heights of 20–80 cm. Each *C. nodosa* domatium is produced together with six new leaves (Yu and Pierce 1998). A *C. nodosa* sapling becomes available for colonization by ants when it produces its first domatium. Thus, I measured the seasonal availability of *A. octoarticulatus* nest sites as the number of *C. nodosa* saplings producing their first domatia throughout the year.

A. octoarticulatus colonies are monogynous (Frederickson 2005). Colony foundation is independent in this species and winged queens disperse by flying. *A. octoarticulatus* queens colonize *C. nodosa* that are not inhabited by ant colonies; they do not replace

established ant colonies on host plants (Yu and Pierce 1998; Yu et al. 2001; Frederickson 2005). *A. octoarticulatus* queens colonize *C. nodosa* at the sapling stage (Yu and Pierce 1998; Frederickson 2005). *A. octoarticulatus* workers protect the young leaves, but not the stems of *C. nodosa* against herbivory (Frederickson 2005).

C. nodosa censuses

In January 2004, five 1-ha plots were established at RNAM. Plots were separated by at least 50 m. Each 1 ha plot was oriented along cardinal directions and divided into four 50-m × 50-m squares. The corners of each plot were marked with PVC tubes and stake flags.

Beginning in January 2004, the population of *C. nodosa* in each plot was censused every month for 13 consecutive months. Each month, the plots were exhaustively searched for all domatia-bearing individuals of *C. nodosa*. Censuses were begun between the 28th and 30th of each month and stretched over a maximum of 7 days. Roughly equal numbers of person-hours (around 40–50 person-hours) were devoted to each monthly search after the first. The first census took longer since both adult and juvenile *C. nodosa* were counted. Subsequent censuses counted the number of juvenile *C. nodosa* that had produced their first domatia since the previous month's census.

Plots were censused by walking each 50-m × 50-m square in each plot back and forth in a series of 2.5-m transects. When a domatia-bearing *C. nodosa* was found, it was numbered and tagged, and its height, number of domatia, and species of ant occupant, if any, were recorded. Plant height was measured using a telescopic measuring rod. Domatia were counted using binoculars when necessary.

In February 2005, all *C. nodosa* in the five plots were visited again and the presence and species identity of ant workers, if any, was recorded. These data were used to determine how many *A. octoarticulatus* colonies had been established in the five plots over the previous year.

A. octoarticulatus colony collections

In January 2004, four hundred *C. nodosa* were found along trails and transects at RNAM, outside the censused plots described above. Each plant was marked and numbered, and its location and species of ant occupant, if any, were recorded. A plant was considered to be occupied by ants if workers could be observed on the plant.

Beginning in February 2004, fifteen *A. octoarticulatus* colonies were collected each month for 12 consecu-

tive months (except in August, when 16 colonies were collected). The colonies collected each month were randomly selected from the subset of the 400 marked *C. nodosa* occupied by *A. octoarticulatus*. On several occasions, an *A. octoarticulatus* colony had died since the initial census or could not be found. When this occurred, an unmarked, haphazardly selected *A. octoarticulatus* colony was collected instead.

All domatia were removed from each *C. nodosa* using tree pruners and then sealed in Ziploc bags. Bags of domatia were stored in an ice chest after collection. Plant height and number of domatia were recorded for each *C. nodosa*. Ant colony collections were made between the 23rd and 30th of the month.

Within 48 h of collection, each domatium was cut open and the contents examined. Each domatium was scored as containing reproductives (with or without workers), workers only, or being empty. The number of queens, female alates, male alates, female alate pupae, male alate pupae, and alate larvae were recorded separately for each domatium containing reproductives. The sexes of the larvae were not determined. All reproductives were collected and stored in 95% ethyl alcohol.

Alate traps

Ant colonies may produce alates some time before mating flights occur. To find out when mating flights occur during the year, traps were set up to catch alates as they arrived at host plants. A total of 21 *C. nodosa* saplings that were not occupied by ants were randomly selected from among the *C. nodosa* saplings present in the initial censuses of the five plots described in *C. nodosa* censuses. Tangletrap was placed over the entrance holes to all the domatia on each plant. The traps were checked every Monday between 3 May 2004 and 28 February 2005, a total of 44 times. Any insects stuck in the Tangletrap were collected. Insects were soaked in mineral oil overnight to remove the Tangletrap, then stored in 95% ethyl alcohol. The Tangletrap on a domatium was replaced whenever it got clogged with debris. Tangletrap was applied to new domatia as they were produced.

All *C. nodosa* saplings used in this part of the study were located at least 1 km, but not more than 5 km, from the ant colonies collected as part of *A. octoarticulatus* colony collections. A minimum distance was maintained so that the collection of adult *A. octoarticulatus* colonies would not interfere with observations of *A. octoarticulatus* alates arriving at traps. A minimum distance of 1 km was chosen because *A. octoarticulatus* disperse over very short distances (Yu et al.

2004). A maximum distance of 5 km was maintained in order to minimize any effect of habitat or climatic differences on comparisons of the timing of alate production and flight.

Statistical analyses

To improve normality, all count and precipitation data were square-root transformed; temperature data were log-transformed (Sokal and Rohlf 1995). To correct for differences in colony size among harvested colonies, the total number of *A. octoarticulatus* reproductives in each colony was divided by the total number of domatia on the plant. Thus, for harvested colonies, monthly and seasonal means of *A. octoarticulatus* reproductives are reported as mean number per domatium.

Following Madigosky and Vatnick (2000) and Miyata et al. (2003), the data were divided into four trimesters that differ in seasonal climate: December–February, March–May, June–August, and September–November. Counts of *A. octoarticulatus* reproductives were compared among trimesters, and counts of *C. nodosa* saplings were compared among plots and among trimesters, using ANOVAs followed by Tukey–Kramer post hoc tests for multiple comparisons. Relationships among monthly means for numbers of *C. nodosa* saplings, *A. octoarticulatus* reproductives, and climatic parameters (rainfall, temperature) were analyzed using linear regression.

The number of queens arriving at traps each week was not normally distributed because of a large number of zeros. For this reason, a Kruskal–Wallis test was used to compare the number of queens arriving at traps among trimesters, and nonparametric correlation coefficients were calculated for the relationships between the number of queens arriving at traps and climate variables. Statistical analyses were conducted in Statview 5.0.1 (SAS Institute).

Results were identical for the relationship between the total number of alates and plant size, whether plant

size was measured as plant height or number of domatia. Only the results using domatia number are presented here.

Results

Weather data

Temperature but not precipitation varied seasonally [ANOVA: maximum daily temperature, $F_{3,337} = 35.305$, $P < 0.0001$; daily precipitation, $F_{3,361} = 0.757$, not significant (NS); the *df* differ because of missing values for maximum temperature]. June–August was the coolest trimester of the year, while March–May was the hottest trimester (Table 1). Total rainfall was 2,890 mm. Mean maximum and minimum temperatures were 30.5 and 24.8°C, respectively.

C. nodosa censuses

In January 2004, a total of 235 domatia-bearing *C. nodosa* plants were found in the five 1-ha study plots. One hundred and forty-seven (63%) *C. nodosa* were occupied by *A. octoarticulatus*, 37 (16%) were occupied by *Azteca* spp., and one (<1%) was occupied by *M. schumannii*. Fifty *C. nodosa* (21%) were not occupied by ants. On average (\pm SE), *C. nodosa* plants were 2.10 ± 0.13 m tall and bore 20.0 ± 1.4 domatia.

Over the following 12 months, 65 new domatia-bearing *C. nodosa* were found in the five plots. All were saplings, bearing four or fewer domatia and measuring less than 1 m tall at first census. The number of new domatia-bearing *C. nodosa* saplings found differed significantly among trimesters, but not among plots (ANOVA: plot, $F_{4,40} = 0.710$, NS; trimester, $F_{3,40} = 9.290$, $P < 0.0001$; interaction term, $F_{12,40} = 0.874$, NS). Between March and May, more *C. nodosa* produced their first domatia than between June and November (Table 1). The mean number of new doma-

Table 1 Means followed by 95% confidence intervals for maximum temperature, precipitation, number of new domatia-bearing *Cordia nodosa* saplings per hectare, and number of *Allomerus*

octoarticulatus alates produced per domatium. Different letters show significantly different trimesters according to Tukey–Kramer post hoc tests ($P < 0.05$)

Variable	December–February	March–May	June–August	September–November
Maximum daily temperature (°C)	30.6 (30.2–31.0) A	31.6 (31.2–32.2) B	29.1 (28.9–29.3) C	30.4 (30.0–30.8) A
Daily precipitation (mm)	2.30 (1.13–3.87) A	3.05 (1.58–4.99) A	3.66 (2.12–5.65) A	2.16 (1.01–3.73) A
<i>C. nodosa</i> saplings (no. ha ⁻¹ month ⁻¹)	0.74 (0.23–1.54) AB	1.95 (1.29–2.75) A	0.11 (0.01–0.34) B	0.17 (0.01–0.53) B
<i>A. octoarticulatus</i> alates produced (no. domatium ⁻¹)	0.49 (0.27–0.78) AB	0.61 (0.37–0.92) A	0.18 (0.09–0.31) B	0.33 (0.15–0.56) AB

tia-bearing *C. nodosa* found each month was significantly correlated with mean maximum temperature (Fig. 1; $r^2 = 0.41$, $P = 0.01$) but not with mean precipitation ($r^2 = 0.10$, NS). When times-series data are used in linear regression, autocorrelation can be a problem because errors may not be independent. However, autocorrelation was not a factor in the significant regression between the number of saplings available for colonization and temperature, according to a Durbin–Watson test for autocorrelation (Durbin–Watson statistic 1.992, NS).

At the final census in 2005, twenty-one new *A. octoarticulatus* colonies had established on *C. nodosa* hosts.

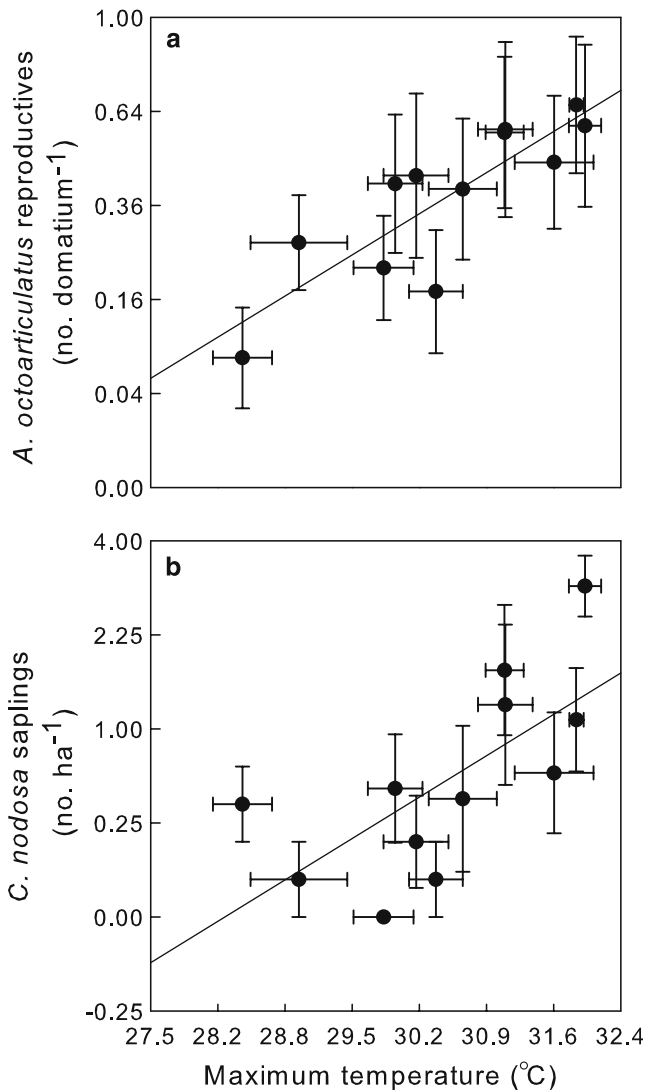


Fig. 1 Mean number (\pm SE) of **a** *Allomerus octoarticulatus* reproductives per domatium and **b** *Cordia nodosa* saplings per hectare produced each month, plotted against mean (\pm SE) daily maximum temperature. Each data point represents 1 month. The x-axis uses a square-root scale, the y-axis a log scale. Solid lines are regression relationships

A. octoarticulatus colony collections

Between February 2004 and January 2005, one hundred and eighty-one *C. nodosa* occupied by *A. octoarticulatus* ants were collected. These bore a total of 5,350 domatia, of which 92% were occupied by ants. Of the 181 *C. nodosa* occupied by *A. octoarticulatus*, 162 were occupied by a single colony, as evidenced by the presence of one *A. octoarticulatus* queen. Seven *C. nodosa* bore two or three queens and associated nestmates; four of these seven *C. nodosa* had less than seven domatia. The remaining 12 *C. nodosa* housed no queen, but *A. octoarticulatus* workers and brood were still present.

A total of 1,880 alate larvae, 1,671 alate pupae, and 1,584 eclosed alates were found in the 181 *A. octoarticulatus* colonies sampled over the year. Thus, I estimated that about 85% (1,584/1,880) of alate larvae reach eclosion. Colonies tended to produce either mostly female alates or mostly male alates (Fig. 2). Over half of the colonies producing alates produced alates of only one sex. More colonies produced only female alates (39 colonies) than only male alates (22 colonies), resulting in a female-biased numerical sex ratio. Of the alate pupae, 57% (947) were female and 43% (724) were male. Of the eclosed alates, 69% (1,089) were female and 31% (495) were male.

Colonies in larger plants had more alates; the total number of alates produced by a colony was significantly correlated with plant domatia number ($r^2 = 0.49$, $P < 0.0001$). Alate sex was also related to plant size. Colonies producing all-female alates were found in smaller plants (average 28.1 domatia, 95% confidence

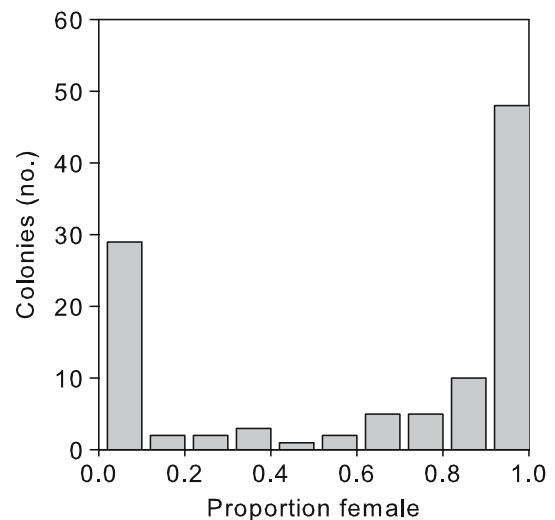


Fig. 2 Frequency distribution of *A. octoarticulatus* sex ratio

interval 23.5–33.1 domatia), than colonies producing all-male alates (average 37.8 domatia, 95% confidence interval 29.9–46.5 domatia; t -test: $t_{55} = 1.97$, $P = 0.05$).

The total number of *A. octoarticulatus* reproductives differed significantly among trimesters (ANOVA: $F_{3,177} = 3.538$, $P = 0.02$). Between March and May, colonies produced significantly more reproductives than between June and August (Table 1). The mean number of alates produced by *A. octoarticulatus* colonies each month was significantly correlated with mean maximum temperature (Fig. 1; $r^2 = 0.72$, $P = 0.0005$), but not mean precipitation ($r^2 = 0.098$, NS). Autocorrelation was not a factor in the significant regression between alate production and temperature (Durbin-Watson statistic 2.436, NS).

Alate traps

The 21 *C. nodosa* with alate traps caught a total of 31 *A. octoarticulatus* queens in 44 weeks. All of the queens caught still had their wings. Alates tended to be caught in the Tangletrap on the youngest domatia. No male *A. octoarticulatus* alates were ever caught. From one to six *A. octoarticulatus* queens were caught together on one plant on the same date, and from one to ten queens were caught on the same plant over the 44 weeks of the study. There was a tendency for alates to be caught in groups on plants. The number of queens caught together on one plant on the same date was significantly aggregated compared to a Poisson distribution (mean = 0.704, variance = 1.56, $\chi^2_1 = 13.2$, $P < 0.001$), as was the number of queens caught on the same plant over 44 weeks (mean = 1.48, variance = 7.56, $\chi^2_2 = 24.9$, $P < 0.001$). Only seven out of 21 plants ever caught alates. Plants that caught alates were significantly larger than plants that did not catch alates (t -test: height, $t_{18} = 2.85$, $P = 0.01$; number of domatia, $t_{18} = 2.77$, $P = 0.01$).

Alate flight showed the same seasonal pattern as alate production. The number of *A. octoarticulatus* queens caught each week differed significantly among trimesters (Kruskal-Wallis test: $H_3 = 10.2$, $P = 0.02$). Alate flight peaked in May, when nine alates were caught, and subsided from June up to and including October, when no alates were caught. The correlation between the number of *A. octoarticulatus* queens caught each week and mean maximum temperature over the previous week was marginally nonsignificant (Kendall correlation: $\tau = 0.197$, $P = 0.06$). There was no correlation between the number of queens caught each week and precipitation over the previous week (Kendall correlation: $\tau = 0.044$, NS).

Reproductive success of *A. octoarticulatus* queens

There were initially 50 unoccupied *C. nodosa* saplings in the five study plots, and 65 *C. nodosa* saplings were produced throughout the year, for a total of 115 *C. nodosa* available to *A. octoarticulatus* queens over 5 ha and 1 full year.

Thirty-one *A. octoarticulatus* queens arrived at 21 *C. nodosa* over the 44 weeks from May 2004 to February 2005, or an estimated 37 queens in 52 weeks. This is an average of 1.7 queens plant⁻¹ year⁻¹. Thus, the 115 *C. nodosa* in the five study plots were visited by an estimated 197 *A. octoarticulatus* queens in 1 year. An average of 6.02 female alates was present in each *A. octoarticulatus* colony collected. Thus, the 147 *A. octoarticulatus* colonies present at the beginning of the study in the five 1-ha plots produced an estimated 885 female alates over the year. Of these 885 female alates, only an estimated 197 successfully located a suitable host plant, for a survival rate of 22%.

Many of the *A. octoarticulatus* queens that arrive at host plants do not survive to found colonies. The final census of the five study plots revealed that only 21 new *A. octoarticulatus* colonies were established over 1 year. After correcting for the fact that 21 of the 115 unoccupied *C. nodosa* in the plots were made unavailable for colonization by the alate traps, an estimated 26 new colonies of *A. octoarticulatus* establish per 5 ha per year. Thus, a mere 26 of the 197 queens that arrive at *C. nodosa* saplings successfully found colonies. This is a survival rate of 13%. In total, a female alate produced by an *A. octoarticulatus* colony has a 2.9% (22% times 13%) chance of surviving to found a colony.

Discussion

Mortality during mating, dispersal, and colony founding

Young *A. octoarticulatus* queens suffer high mortality during mating, dispersal, and colony founding. Only 3% survive. This does not compare favorably to queen survival before emergence from the maternal nest, which is about 85% from the larval stage to eclosion. Nor does it compare favorably to the survival of queens in established colonies, which is almost 90% per year (M. E. Frederickson, unpublished data). Thus, mating, dispersal, and colony founding are more perilous for *A. octoarticulatus* queens than other life cycle stages. The same is true in many other ant species (Hölldobler and Wilson 1990; Sommer and Hölldobler 1995; Gordon and Kulig 1996).

In this study, I estimated the mortality of *A. octoarticulatus* queens separately: (1) from the time queens leave their maternal nests until they arrive at host plant saplings (mating and dispersal), and (2) from the time queens arrive at host plant saplings until they produce workers (colony founding). *A. octoarticulatus* queen mortality was substantial during both stages, around 78 and 87%, respectively.

During mating and dispersal, queen mortality may be a result of predation, parasitism, starvation, or desiccation (Nichols and Sites 1991; Gordon and Kulig 1996; Nery and Vasconcelos 2003; Wiernasz and Cole 2003), although the latter is unlikely to be important in a rainforest species such as *A. octoarticulatus*. The length of time a queen spends outside the nest probably increases her risk of mortality. Thus, queens who can quickly find mates and nest sites should improve their chances of surviving.

Competition among queens for nest sites

The results presented here provide evidence that *A. octoarticulatus* queens compete intraspecifically for host plants. Many *A. octoarticulatus* queens arrived to colonize individual *C. nodosa* saplings. However, by the time workers were evident on a small *C. nodosa*, only occasionally did the plant hold more than one *A. octoarticulatus* queen. At maturity, each *C. nodosa* plant hosted only one monogynous *A. octoarticulatus* colony. This pattern suggests that *A. octoarticulatus* queens compete for hosts, a common occurrence among plant-ant species (Davidson et al. 1989).

Moreover, *A. octoarticulatus* queen mortality during colony founding may be caused almost entirely by competition among queens. Over the course of this study, 31 queens were caught on seven *C. nodosa* saplings. At maturity, these seven *C. nodosa* plants could host a maximum of seven colonies. This implies a mortality rate of 77% (1–7/31) due to competition among queens on the same plant. Thus, competition may account for most of the 87% mortality of queens after arriving at hosts.

Despite competition for hosts, the host plant population was not saturated. Twenty percent of *C. nodosa* were not occupied by ants and only seven out of 21 *C. nodosa* with traps caught *A. octoarticulatus* queens. The apparent contradiction between the availability of host plants and the arrival of multiple queens at individual saplings is resolved if not all host plants are suitable for colonization by ants. In this study, saplings were either never colonized by queens, or colonized repeatedly by queens, suggesting some saplings are more desirable than others to queens. Plant size is one

factor that may affect the desirability of plants to queens; plants that were colonized by queens were larger than plants that were not colonized by queens.

Alternatively, it is possible that dispersal limitation, and not nest site quality, determines whether queens colonize hosts. Dispersal limitation, or the failure of queens to arrive at suitable, but spatially isolated host plants, has been demonstrated in a few plant-ant species (Vasconcelos 1993), including *A. octoarticulatus* (Yu et al. 2004). The relative importance of dispersal limitation and nest site quality to queen colonization of saplings requires further investigation.

Sex ratio

The sex ratio of a population is sensitive to sex-bias in both dispersal and competition for limiting resources such as nest sites or mates (Frank 1987). Local resource competition (LRC) occurs when dispersal limitation leads to competition among related females for resources; local mate competition (LMC) occurs when dispersal limitation leads to competition among related males for mates (Clark 1978; Frank 1987). As investment in reproduction increases, LRC tends to increase male bias in the sex ratio, while LMC tends to increase female bias, because of diminishing returns from investments in the dispersal-limited sex (Frank 1987).

In general, plant-ants like *A. octoarticulatus* are good candidates for LRC, because of limited dispersal by queens and fierce competition among queens for hosts. However, the only studies of sex ratio in plant-ants found evidence for LMC, not for LRC (Fonseca 2000; Gaume and McKey 2002). In fact, there are few examples of LRC occurring in any invertebrates (Bourke and Franks 1995; Dagg and Vidal 2004; Kümmerli et al. 2005).

Like many other ant species, *A. octoarticulatus* colonies produced either mostly female or mostly male alates (Bourke and Franks 1995). Colonies producing females were significantly smaller than colonies producing males. Colony size was measured by the number of domatia on the colony's host plant, a reasonable approximation because 92% of domatia were occupied by ants. The pattern that smaller colonies produce mostly females, and larger colonies produce mostly males is suggestive of LRC. However, a closer examination of investment (not numerical) sex ratios is necessary to establish that LRC is at work in *A. octoarticulatus*.

It is not known where mating occurs in *A. octoarticulatus*. One possibility is that females and males both search out *C. nodosa* saplings and mate on or near

young host plants. However, no *A. octoarticulatus* males were ever caught on the domatia of the *C. nodosa* saplings in this study, suggesting this is not the case. Another possibility is that *A. octoarticulatus* alates mate on or near their maternal host plant. A better understanding of the mating behavior of *A. octoarticulatus* would shed light on the distances sexuals travel to find mates, and hence on whether sex-biased dispersal limitation affects sex ratio in this species.

Reproductive phenology of an obligate plant-ant

The seasonal pattern of production and flight of *A. octoarticulatus* alates matched the seasonal availability of their nest sites, domatia-bearing *C. nodosa* saplings. While the evidence is only correlative, the results suggest that *A. octoarticulatus* colonies synchronize their reproduction to the emergence of domatia on *C. nodosa* saplings, as suggested by Fonseca (1999). The reverse is also possible, but less likely because *C. nodosa* hosts several ant species with different reproductive phenologies (M. E. Frederickson, unpublished data).

The production of domatia by *C. nodosa* saplings showed a seasonal pattern. Most saplings produced their first domatia between March and May. Thus, more domatia-bearing *C. nodosa* saplings were available for colonization by ants at this time of year than at other times. To my knowledge, only one other study has examined whether host plant availability shows a seasonal pattern in an ant-plant. Murase et al. (2002) found no obvious seasonal trend in the abundance of *Macaranga* seedlings suitable for colonization by *Crematogaster* ants.

Domatia production by *C. nodosa* saplings, which occurs together with leaf production, was correlated with temperature, but not rainfall. This suggests that temperature, or a correlated variable such as light intensity, determines the phenology of domatia production in *C. nodosa*. In forests like RNAM with little or no dry season, light intensity has been shown to limit leaf production, and leaves are produced in the season of peak irradiance (van Schaik et al. 1993; Wright and van Schaik 1994; Graham et al. 2003). *C. nodosa* is a small-statured plant species—both saplings and mature trees of this species live in the light-limited rainforest understory. Thus, light availability may limit the production of domatia and leaves by *C. nodosa*, resulting in greater domatia production during months with greater light intensity and higher temperatures.

The production and flight of *A. octoarticulatus* sexuals also showed a strong seasonal pattern, again peaking from March to May. Two other studies have

investigated the reproductive phenologies of plant-ants. Janzen (1967) found that *Pseudomyrmex ferruginea*, which inhabits the ant-plant *Acacia cornigera*, reproduces continuously throughout the year, although alates do not fly in cool weather, while Vasconcelos (1993) found that *Pheidole minutula*, which inhabits the ant-plant *Maieta guianensis*, reproduces predominantly during the rainy season.

Both *A. octoarticulatus* alate production and flight were correlated with temperature, but not precipitation. The correlation with temperature was strong for alate production, but weak and marginally nonsignificant for alate flight. Alate flight was measured as the number of queens arriving at a host plant, so it was probably subject to a range of factors affecting the ability of alates to survive the mating flight and successfully locate a host. It is also possible that temperature works in combination with other cues to determine when alates leave the nest on their mating flights. Nonetheless, colonies clearly produced more reproductives in warmer weather. Temperature may have a direct effect on alate production, or it may be a proximate cue by which *A. octoarticulatus* coordinates reproduction to nest site availability. The latter has two benefits for *A. octoarticulatus*. Any synchronization makes it easier to find mates (Kaspari et al. 2001b), and synchronization with host plant availability makes it easier to find nest sites, a limiting resource for this species. Why does *A. octoarticulatus* still produce some reproductives from June to November, when host plants and mates are rare? One possibility is that alates produced in the off-peak might escape competition for the few nest sites available then.

In this study, queen mortality during mating and dispersal, which probably depends on the time queens spend searching for host plants, was similar to queen mortality due to competition during colony founding. This indicates that two aspects of nest site availability—the number of available nests and competition for those nests—may determine reproductive success in *A. octoarticulatus* and give rise to this species' reproductive phenology. How does this compare to other tropical ant species? Kaspari et al. (2001a) examined the reproductive phenologies of 81 ant species on Barro Colorado Island (BCI), Panama. There do not appear to be any obligate plant-ants among the species they studied, though, some of the ants that were identified only to morphospecies belong to genera that include plant-ants. Kaspari et al. (2001a) found that congeneric species reproduced at similar times in the year, with most species reproducing during the rainy season. Congeners often have similar nesting habits, and the rainy season provides ant queens on BCI with soft soil,

deep litter, and thick vegetation (Kaspari et al. 2001a). Thus, nest site availability may determine reproductive phenology in many tropical ant species.

In tropical rainforests, colonization sites can be limiting for many organisms. For example, the regeneration of many tropical trees depends on the formation of gaps (Denslow 1987; Wright et al. 2003). Like ant queens, plant propagules often must reach and establish in scarce colonization sites in order to succeed. How gap dynamics influence the life histories of tropical trees has received considerable attention from ecologists (Denslow 1987; Clark and Clark 1992; Wright et al. 2003). The present study is among the first to consider how patterns in the availability of colonization sites shape the life history of a sessile tropical animal.

Acknowledgements I thank D. Gordon for suggesting many improvements to this manuscript, and for providing the idea to catch alates as they arrive at saplings. J. Bronstein, K. Fitzgerald, C. Fonseca, and one anonymous reviewer also provided many helpful comments on this manuscript. A. Coral and J. Silva provided invaluable assistance in the field. I thank the Instituto Nacional de Recursos Naturales and the Instituto de Investigaciones en la Amazonia Peruana in Peru for permission to carry out this study. I also thank the Stanford Graduate Fellowships, the National Science and Engineering Research Council of Canada, and Stanford University's Center for Evolutionary Studies for financial support.

References

- Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton, N.J.
- Clark AB (1978) Sex ratio and the local resource competition hypothesis in a prosimian primate. *Science* 201:163–165
- Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol Monogr* 62:315–344
- Dagg JL, Vidal S (2004) Sex ratio adjustment and maternal condition in two aphid species. *Behav Ecol Sociobiol* 55:231–235
- Davidson DW, McKey D (1993) The evolutionary ecology of symbiotic ant–plant relationships. *J Hym Res* 2:13–83
- Davidson DW, Snelling RR, Longino JT (1989) Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21:64–73
- Davidson DW, Foster RB, Snelling RR, Lozada PW (1991) Variable composition of some tropical ant–plant symbioses. In: Price PW, Lewinsohn TM, Wilson Fernandes G, Benson WW (eds) Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York, pp 145–162
- Denslow JS (1987) Tropical rainforest gaps and tree species diversity. *Annu Rev Ecol Syst* 18:431–451
- Fiala B, Maschwitz U (1990) Studies on the South East Asian ant–plant association *Crematogaster borneensis*/*Macaranga*: adaptations of the ant partner. *Insect Soc* 37:212–231
- Fonseca CR (1999) Amazonian ant–plant interactions and the nesting space limitation hypothesis. *J Trop Ecol* 15:807–825
- Fonseca CR (2000) Cooperação, conflitos e razão sexual em himenópteros sociais: a perspectiva de uma formiga amazônica. In: Martins RP, Lewinsohn TM, Barbeitos MS (eds) *Ecologia e comportamento de Insetos. Série Oecologia Brasiliensis*, vol VIII. PPGE-UFRJ, Rio de Janeiro, pp 131–148
- Frank SA (1987) Variable sex ratio among colonies of ants. *Behav Ecol Sociobiol* 20:195–201
- Frederickson M (2005) Ant species confer different partner benefits on two neotropical myrmecophytes. *Oecologia* 143:387–395
- Gaume L, McKey D (2002) How identity of the homopteran trophobiont affects sex allocation in a symbiotic plant–ant: the proximate role of food. *Behav Ecol Sociobiol* 51:197–205
- Gentry AH (1988) Tree species richness of upper Amazonian forests. *Proc Natl Acad Sci USA* 85:156–159
- Gordon DM, Kulig AW (1996) Founding, foraging and fighting: relationships between colony size and the spatial distribution of harvester ant nests. *Ecology* 77:2393–2409
- Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright JS (2003) Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proc Natl Acad Sci USA* 100:572–576
- Heil M, McKey D (2003) Protective ant–plant interactions as model systems in ecological and evolutionary research. *Annu Rev Ecol Evol Syst* 34:425–453
- Hölldobler B, Wilson EO (1990) The ants. Belknap, Cambridge
- Janzen DH (1967) Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *Kans Univ Sci Bull* 47:315–558
- Janzen DH (1973) Evolution of polygynous obligate acacia-ants in western Mexico. *J Anim Ecol* 42:727–750
- Kaspari M, O'Donnell S, Kercher JR (2000) Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *Am Nat* 155:280–293
- Kaspari M, Pickering J, Longino JT, Windsor D (2001a) The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. *Behav Ecol Sociobiol* 50:382–390
- Kaspari M, Pickering J, Windsor D (2001b) The reproductive flight phenology of a neotropical ant assemblage. *Ecol Entomol* 26:245–257
- Kümmerli R, Helms KR, Keller L (2005) Experimental manipulation of queen number affects colony sex ratio investment in the highly polygynous ant *Formica exsecta*. *Proc R Soc B* 272:1789–1794
- Levings SC, Franks NR (1982) Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63:338–344
- Madigosky SR, Vatnick I (2000) Microclimatic characteristics of a primary tropical Amazonian rain forest, ACEER, Iquitos, Peru. *Selbyana* 21:165–172
- Miyata H, Shimamura T, Hirotsawa H, Higashi S (2003) Morphology and phenology of the primitive ponerine army ant *Onychomyrmex hedleyi* (Hymenoptera: Formicidae: Ponerinae) in a highland rainforest of Australia. *J Nat Hist* 37:115–125
- Murase K, Itioka T, Inui Y, Itino T (2002) Species specificity in settling-plant selection by foundress ant queens in *Macaranga-Crematogaster* myrmecophytism in a Bornean dipterocarp forest. *J Ethol* 20:19–24
- Nery AS, Vasconcelos HL (2003) Growth and survival of incipient ant colonies in two Amazonian ant-plants: effect of habitat, host plant, and mode of colony founding (Hymenoptera: Formicidae). *Sociobiology* 42:151–162
- Nichols BJ, Sites RW (1991) Ant predators of founder queens of *Solenopsis invicta* (Hymenoptera, Formicidae) in central Texas. *Environ Entomol* 20:1024–1029
- Phillips OL, Hall P, Gentry AH, Sawyer SA, Vásquez R (1994) Dynamics and species richness of tropical rain forests. *Proc Natl Acad Sci USA* 91:2805–2809

- Philpott SM, Foster PF (2005) Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. *Ecol Appl* 15:1478–1485
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annu Rev Ecol Syst* 16:179–214
- van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu Rev Ecol Syst* 24:353–377
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Sombroek W (2001) Spatial and temporal patterns of Amazon rainfall: consequences for planning of agricultural occupation and the protection of primary forests. *Ambio* 30:388–396
- Sommer K, Hölldobler B (1995) Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*. *Anim Behav* 50:287–294
- Stanton ML, Palmer TM, Young TP (2002) Competition-colonization trade-offs in a guild of African acacia-ants. *Ecol Monogr* 72:347–363
- Stanton ML, Palmer TM, Young TP (2005) Ecological barriers to early colony establishment in three coexisting acacia-ant species in Kenya. *Insect Soc* 52:393–401
- Torres JA (1984) Niches and coexistence of ant communities in Puerto Rico: repeated patterns. *Biotropica* 16:284–295
- Vasconcelos HL (1993) Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant. *Oecologia* 95:439–443
- Vieira S, Barbosa de Camargo P, Selhorst D, da Silva R, Hutyra L, Chambers JQ, Brown IF, Higuchi N, dos Santos J, Wofsy SC, Trumbore SE, Martinelli LA (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140:468–479
- Wiernasz DC, Cole BJ (2003) Queen size mediates queen survival and colony fitness in harvester ants. *Evolution* 57:2179–2183
- Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. *Am Nat* 143:192–199
- Wright SJ, Muller-Landau HC, Condit R, Hubbell SP (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185
- Yu DW, Pierce NE (1998) A castration parasite of an ant-plant mutualism. *Proc R Soc Lond B* 265:75–82
- Yu DW, Wilson HB, Pierce NE (2001) An empirical model of species coexistence in a spatially structured environment. *Ecology* 82:1761–1771
- Yu DW, Wilson HB, Frederickson ME, Palomino W, De la Colina R, Edwards D, Balareso A (2004) Experimental demonstration of species coexistence enabled by dispersal limitation. *J Anim Ecol* 73:1102–1114