Seasonal and Nocturnal Periodicities in Ant Nuptial Flights in the Tropics (Hymenoptera: Formicidae)

by

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ABSTRACT

Nocturnal nuptial flights of ants were studied at Guaynabo and Guánica in the tropical island of Puerto Rico. A great proportion of the species had a high frequency of flights during the year with little seasonality in the frequency of flights. Flights were less frequent during the dry season. Nuptial flights at Guaynabo occurred mostly during the post-sunset (18:30-22:30) and pre-dawn (04:00-06:00) hours. Few flights occurred between these two periods. The number of flights was fewer and flights on the average smaller in size in the Guánica dry forest than at Guaynabo. There was little differentiation in the flight patterns of species belonging to the same genus. All-male flights were more common than all-female flights, but in some species the pattern was reversed. One-sex flights were commoner than flights in which both sexes were present. Usually more males were captured on a nuptial flight than females, but in some months or in some species the pattern was reversed. The lack of flight synchronization between the sexes results in a great loss of reproductive effort in most species. This lack of synchronization implies that mating success cannot be estimated by the relative abundance of queens and males in nests.

Key words: ants, dry forest, nuptial flights, Puerto Rico, sex ratio, seasonality, tropics.

INTRODUCTION

Ants have different ways to establish new colonies. Many species have winged alates that participate in nuptial flights, and after copulation the young queens establish a new colony. Species in which females fly toward male aggregations have tightly synchronized flights (Hölldobler & Wilson 1990). In some species, one sex has lost the capacity to fly and mating occurs in or near the nest. When females are

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wingless, they attract the winged males; and nuptial flights do not appear to be well synchronized (Hölldobler & Wilson 1990). Other species practice colony budding in which reproductives are accompanied by workers to establish a new colony.

Most data on ant nuptial flights deal with species from temperate zones (Clark & Hainline 1975, Yamauchi *et al.* 1986, Woyciechowski 1990), and a great proportion of the information is based on the observation of only one flight or swarm event (e.g., Tarpley 1965, Amante 1972, Little 1980, Elmes & Webb 1985). Deyrup & Trager (1986) present information about nuptial flights for several tropical species; but data about the frequency, size and the sex ratio in the flights are not presented. There are few long-term studies of nuptial flights in tropical areas, and all deal with male army ants (Haddow *et al.* 1966, Kannowski 1969, Leston 1979). Apparently, the large size of army ant males and the lack of taxonomic information relating queens to workers in other ant species have been reasons for the restriction of nuptial flight studies to army ants in tropical areas. Because army ant queens are so different from other ant queens (Gotwald 1995), it is unknown if army ant mating flight patterns are typical of tropical ants.

On many occasions information is presented on mating flights (e.g., day or night), but the specific time of the day is not indicated. Exceptions to this pattern are the works of Haddow *et al.* (1966), Boomsma & Leusink (1981), Yamauchi *et al.* (1986) and Plateaux (1987) which report temporal spacing of species. Temporal segregation of flights has been suggested as a mechanism to prevent interspecific hybridization (Hölldobler & Wilson 1990).

Nuptial flights of ants occur at species-characteristic times of the day (McCluskey 1965). Although the time at which flights occur is programmed by a species-specific diel rhythm (Hölldobler & Wilson 1990), the ants need external cues to synchronize the flights (McCluskey 1963, Weber 1972). Weather conditions (rain, humidity, temperature, light intensity and low wind speed) have been found to play a role in the timing of nuptial flights for many species (Moser 1967, Kannowsky 1969, Weber 1972, Clark & Hainline 1975, Yamauchi *et al.* 1986, Milio *et al.* 1988). Rain preceded by a period of dry weather is a common triggering stimulus in species that occupy dry habitats (Markin *et al.* 1971, Kannowski 1972, Rust 1988). Mating after rains facilitates excavation, and queens are protected from desiccation due to overheating (Hölldobler & Wilson 1990). Nuptial flight synchronization for a particular ant species has been associated with predator avoidance, maintenance of reproductive isolation and outbreeding promotion (Nagel & Rettenmeyer 1973, Bourke & Franks 1995).

Most temperate zone ant species have nuptial flights at most for one or two months, and flights do not occur on a nearly daily basis (Tarpley 1965, Baldridge *et al.* 1980, Yamauchi *et al.* 1986). Few flights per year occur in *Pogonomyrmex* (Nagel & Rettenmeyer 1973, Clark & Hainline 1975, Rust 1988), *Lasius* and *Myrmica* (Boomsma & Leusink 1981). One of the few exceptions is *Camponotus pennsylvanicus*, in which nuptial flights can last up to five months, but most flights occur during spring and generally involve a limited number of queens (Fowler & Roberts 1982). Mostly the summer months are preferred for nuptial flights by temperate zone ants (Boomsma & Leusink 1981). Studies of nuptial flights in temperate ant species have influenced interpretations about the adaptive significance of flights. Bourke and Franks (1995) suggest that "The typical large scale and infrequency of nuptial flights (roughly two or three per year) are further evidence for their role in inbreeding avoidance." Even in tropical areas, Weber (1972) indicates that attine nuptial flights occur during a limited season of the year.

There is a large literature dealing with sexual investment and numerical sex ratio in ants (reviewed by Bourke & Franks 1995, Crozier & Pamilo 1996). Given the wealth of contributing factors, testing sex allocation in social Hymenoptera is not simple. Polygyny, polydomy, colony budding, worker reproduction and local resource competition affect sex ratio investment in ants (Bourke & Franks 1995). The simplest case to model is monogynous ants without worker reproduction. Here the numerical sex ratio is male biased, but the investment ratio is female-biased (workers the controlling party) because the energetic costs of raising females are greater than for males. Male biased numerical sex ratio occurs in polydomous, polygynous species, and in those that establish new colonies by budding or fission (Keller & Passera 1992, Bourke & Franks 1995). Among the factors affecting the inclusive fitness of an individual is the mating success of females and males. Mating success depends on the numerical sex ratio (alate males usually mate once and do not fight to monopolize females — Heinze & Hölldobler 1993) in a swarm and that information is generally lacking.

The reproductive behavior of ants is a poorly explored domain and more studies are needed in the comparative natural history of nuptial flights (Hölldobler & Wilson 1990). In this study we present the nocturnal and seasonal periodicities of nuptial flights in two areas on the tropical island of Puerto Rico. Also, we provide information about the numerical sex ratio in these flights and its consequences on mating success.

SITE DESCRIPTIONS

We studied the nocturnal nuptial flights of ants at two sites in Puerto Rico. Puerto Rico is one of the islands comprising the Greater Antilles. It is about 160 km long and 55 km wide, with a highly mountainous topography . One site was located at Barrio Sonadora, Guaynabo (18°17'N 66°07'W) in the subtropical moist forest life zone (Ewel & Whitmore 1973). The vegetation consists mainly of pasture land intermixed with patches of secondary forest. Mean annual precipitation is around 1950 mm with a short dry season from January to April. Mean annual temperature is approximately 24.5 °C. The second site was located in the subtropical dry forest in Guánica, Puerto Rico (17°58'N 66°52'W). The Guánica dry forest has a low and variable annual rainfall (772 mm, CV of 35.1) (Castilleja 1991). The period from January to March is usually the driest and moisture is typically limited during mid to late summer (Murphy & Lugo 1986). Forty-five percent of the annual precipitation occurs during the months of September, October and November (Castilleja 1991). The maximum mean temperature (28 °C) in the forest occurs from August to October and the minimum (24 °C) between January and February. The ant community consists of 46 species in the Guánica dry forest and 47 at Guaynabo.

METHODS

Ants in nuptial flights were collected with light traps (BioQuip trap with a 22-watt circline black light). A 4 mm wire mesh screen was laid over the bottom of the funnel to keep unwanted insects from the interior of the trap. Specimens were collected in a jar containing 70% ethanol. In Guaynabo the light traps were operated at three periods of time during the night: 18:30 to 22:30 (post-sunset), 01:00 to 03:00 and from 04:00 to 06:00 (pre-dawn) hours. The post-sunset light trap was on every night from 1 August 1995 to 31 July 1996 (except for one night in Oct-95, Nov-95, Dec-95, Jul-96, and two nights in May-96) and from 1 July 1999 to 30 September 1999. Samples from September 1995 were lost in the mail, and data for that month were excluded from the analyses. The 01:00 to 03:00 hour trap was operated from 1 July 1996 to 30 November 1996 (except one night in July and six nights in September). The pre-dawn trap was in operation from 4 June to 10 August 1996 and from 1 October 1999 to 30 September 2000. The Guánica light trap was in operation for the entire night from 8 April 1996 to 26 December 1997 (except one night in Jul-96, Aug-97, and six nights in Sept-96 because passage of tropical storm Hortense interrupted the electricity). Ants were identified as to species and sex under a stereo zoom microscope. We counted all individuals collected except the members of the following four species: *Camponotus kaura*, *C. taino*, *Myrmelachista ramulorum* and *Pheidole moerens* (post-sunset at Guaynabo from August 1995 to July 1996). For these four species we classified the flights in the following categories: small (less than 20 males or females), medium (more than 20 but less than 100), and large (over 100 females or males). During 1999 all individuals collected from 18:30 to 22:30 hours at Guaynabo were counted including the above four species.

We measured daily temperature and precipitation at Guánica. At Guaynabo we took the temperature at 06:00 hours and made qualitative observations of rain intensity for the post-sunset and pre-dawn periods. Information on wind speed was obtained from the National Weather Service report for the San Juan area.

RESULTS

Sixty six percent (31 of 47) of the ant species present at the Guaynabo site and 78% of the species (36 of 46) at the Guánica dry forest had nocturnal nuptial flights. The ant flights at Guaynabo were organized into two groups: the post-sunset (18:30-22:30 hours) (Table 1) and the pre-dawn (04:00-06:00 hours) (Table 4). The species with nuptial flights in the post-sunset period tended to have the most frequent and the largest flights (Table 2). Nuptial flights occurred in 96.4% (N = 422) of the nights. A total of 1,696 flights occurred in a period of 422 nights with an average of 4.0 flights per night. Species with more than one hundred nuptial flights (Table 3) included the ponerine *Odontomachus ruginodis* (287); the formicines: *Myrmelachista ramulorum* (283), *Camponotus kaura* (147), *C. sexguttatus* (103); and the myrmicines *Pheidole moerens* (279) and *Solenopsis geminata* (267). Apparently stray individuals of the following species, which had nuptial flights during the pre-dawn period, were collected in the post-sunset period (Q = queens, M = males): *Brachymyrmex heeri* (1Q:6M), *Pheidole sculptior* (1Q), *P. subarmata* (5Q:2M), *Pseudomyrmex simplex* (1M), *Solenopsis azteca* (5M), *Tapinoma melanocephalum* (3M), *Wasmannia auropunctata* (4Q:33M), and *W. sigmoidea* (1Q:1M).

There was little seasonality in the number of flights in the post-sunset group (Table 1). The total number of flights per month (for all species and at least one sex flying during a night) was fewer from January to May, corresponding to months with low rainfall and relatively low temperatures. The temperature fluctuated from 16°C to 24.4°C during these months (maximum temperature at 06:00 was 26.6°C in August). Species in the genera *Camponotus* and *Hypoponera*

Table 1. Number of flights, listed by sex (Q = queens, M = males) and month, for species which flew from 18:30 to 22:30 hours at Guaynabo in 422 nights. The last three columns correspond to 1999. Dashes indicate no flights.

Species (sex)	Aug-95	Oct-95	Nov-95	Dec-95	Jan-96	Feb-96	Mar-96	Apr-96	May-96	Jun-96	Jul-96	Jul-99	Aug-99	Sep-99
Brachymyrmex obscurior (M)	1	1	—	—	—	—	—	—	1	—	1	5	—	—
Camponotus kaura (Q)	7	4	5	3	—	1	2	1	—	4	10	10	2	2
Camponotus kaura (M)	18	7	6	5	2	3	6	5	11	12	16	22	15	13
Camponotus sexguttatus (Q)	8	3	2	1	—	2	—	—	—	3	5	4	3	3
Camponotus sexguttatus (M)	15	7	4	4	2	1	3	5	3	8	11	9	12	14
Camponotus taino (Q)	4	1	1	1	—	—	—	—	—	4	7	9	2	—
Camponotus taino (M)	11	3	3	1	1	2	3	1	6	11	8	12	11	9
Hypoponera opaciceps (Q)	—	8	10	13	8	1	—	—	—	—	—	1	3	6
Hypoponera opacior (M)	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Hypoponera punctatissima (Q)	—	9	14	22	6	4	1	1	—	—	—	—	—	—
Linepithema melleum (Q)	—	—	1	—	—	—	—	—	—	—	—	1	—	—
Linepithema melleum (M)	1	—	2	3	2	3	2	1	2	—	1	2	—	1
Monomorium ebeninum (M)	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Mycocepurus smithii (Q)	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Myrmelachista ramulorum (Q)	16	15	20	13	10	8	12	7	13	7	15	11	15	15
Myrmelachista ramulorum (M)	22	24	23	22	20	19	22	14	15	14	21	21	22	20
Odontomachus ruginodis (Q)	6	8	16	16	6	13	12	13	16	8	15	6	3	2
Odontomachus ruginodis (M)	21	14	12	6	9	5	15	21	25	28	27	24	24	18
Paratrechina longicornis (Q)	2	1	—	—	—	—	—	—	—	—	—	2	—	—
Paratrechina longicornis (M)	14	7	2	5	2	—	1	2	1	6	9	6	2	3
Paratrechina myops (Q)	2	—	—	—	—	—	—	—	—	—	2	1	—	1
Paratrechina myops (M)	2	4	—	4	3	—	—	—	—	—	4	1	1	—
Paratrechina steinhelli (Q)	—	1	1	1	—	—	—	—	—	1	—	—	—	—
Paratrechina steinhelli (M)	1	1	4	1	1	—	—	—	1	1	3	—	—	1
Phaidole moerens (Q)14	16	13	13	7	5	5	12	13	12	10	11	11	12	
Pheidole moerens (M)	19	22	26	24	18	9	10	21	18	18	20	25	20	21
Solenopsis geminata (Q)13	8	10	10	12	12	9	6	13	20	17	11	9	10	
Solenopsis geminata (M)19	13	23	18	17	13	10	19	17	20	16	11	12	14	
Tetramorium bicarinatum (Q)	—	—	2	—	—	—	—	—	—	1	—	1	—	—
Total flights in a month[a]	151	130	141	145	100	75	81	91	104	125	148	151	128	126
Average flights per night[a]	4.9	4.3	4.9	4.8	3.2	2.6	2.6	3.0	3.6	4.2	4.9	4.9	4.1	4.2

[a] Indicates all species

In *Pheidole moerens* (Q), *Solenopsis geminata* (Q) and *Solenopsis geminata* (M) all figures need to be move one column to the right. The 14, 13 and 19 contiguous to each species name correspond to Aug 95, the 16, 8 and 13 correspond to Oct 95 and so on.

Table 2. Frequency of nuptial flights and relative abundance of alates (Q = queens, M = males) trapped at Guaynabo (18:30-22:30 hours) during 422 nights. Mean and total alates for *Camponotus kaura*, *C. taino*, *Pheidole moerens* and *Myrmelachista ramulorum* are based on 92 nights of records.

Species (sex)	No. of flights	Max. alates in a night	Mean ± SD alates/flight	Total alates
Brachymyrmex obscurior (M)	9	5	1.8 ± 1.3	16
Camponotus kaura (Q)	51	62	16.4 ± 19.6	229
Camponotus kaura (M)	141	532	78.2 ± 142.1	3909
Camponotus sexguttatus (Q)	34	5	2.0 ± 1.3	68
Camponotus sexguttatus (M)	98	189	9.1 ± 24.5	894
Camponotus taino (Q)	29	38	13.5 ± 14.4	148
Camponotus taino (M)	82	671	96.3 ± 183.7	3080
Hypoponera opaciceps (Q)	50	29	3.9 ± 5.5	197
Hypoponera opacior (M)	1	10	10.0 ± 0.0	10
Hypoponera punctatissima (Q)	57	18	3.6 ± 3.8	206
Linepithema melleum (Q)	2	1	1.0 ± 0.0	2
Linepithema melleum (M)	20	40	8.0 ± 9.6	159
Monomorium ebeninum (M)	1	1	1.0 ± 0.0	1
Mycocepurus smithii (Q)	1	1	1.0 ± 0.0	1
Myrmelachista ramulorum (Q)	177	98	11.8 ± 20.4	484
Myrmelachista ramulorum (M)	279	902	134.0 ± 183.9	8444
Odontomachus ruginodis (Q)	140	36	2.7 ± 3.9	379
Odontomachus ruginodis (M)	249	29	4.6 ± 5.0	1146
Paratrechina longicornis (Q)	5	1	1.0 ± 0.0	5
Paratrechina longicornis (M)	60	21	2.5 ± 3.1	152
Paratrechina myops (Q)	6	4	1.7 ± 1.2	10
Paratrechina myops (M)	19	5	1.6 ± 1.2	31
Paratrechina steinheili (Q)	4	2	1.3 ± 0.5	5
Paratrechina steinheili (M)	14	8	2.0 ± 2.0	28
Pheidole moerens (Q)	154	10	2.7 ± 2.4	93
Pheidole moerens (M)	271	133	20.5 ± 27.4	1355
Solenopsis geminata (Q)	160	20	2.5 ± 3.1	405
Solenopsis geminata (M)	222	54	6.1 ± 9.1	1357
Tetramorium bicarinatum (Q)	4	1	1.0 ± 0.0	4

exhibited the greatest seasonality. *Camponotus kaura* and *C. taino* had only two flights (out of 42) containing more than 20 individuals from January to April and had the largest nuptial flights from June to September (mostly in the summer). Only two queens of *C. sexguttatus* were collected from January to May, and the number of males was low compared to other months. *Hypoponera opaciceps* and *H. punctatissima* concentrated their flights from September to January. In *Pheidole moerens* only 7 flights (out of 60) contained above 20 individuals from January to April; the largest flights of *P. moerens* occurred in May, June, October and November.

With the exception of *Hypoponera opaciceps*, *H. punctatissima*,

Table 3. Nuptial flights in which only males, only females, or both sexes were trapped from 18:30 to 22:30 hours at Guaynabo in 422 nights. Dashes indicate no flights.

Species	All-male flights	All-female flights	Both sexes	Total flights
Brachymyrmex obscurior	9	—	—	9
Camponotus kaura	96	6	45	147
Camponotus sexguttatus	69	5	29	103
Camponotus taino	54	1	28	83
Hypoponera opaciceps	—	50	—	50
Hypoponera opacior	1	—	—	1
Hypoponera punctatissima	—	57	—	57
Linepithema melleum	18	—	2	20
Monomorium ebeninum	1	—	—	1
Mycocepurus smithii	—	1	—	1
Myrmelachista ramulorum	106	4	173	283
Odontomachus ruginodis	147	38	102	287
Paratrechina longicornis	59	4	1	64
Paratrechina myops	18	5	1	24
Paratrechina steinheili	12	2	2	16
Pheidole moerens	125	8	146	279
Solenopsis geminata	107	45	115	267
Tetramorium bicarinatum	—	4	—	4

Mycocepurus smithii and *Tetramorium bicarinatum*, in which no males were captured in the post-sunset period, males flew on more nights than females (Table 2). We have found only ergatoid males, which do not fly, in *H. punctatissima* and *H. opaciceps*. For species in which both sexes were captured, the numerical sex ratios usually were strongly biased in favor of males (Table 2). Queens of *Brachymyrmex obscurior*, *H. opacior* and *Monomorium ebeninum* (queens are ergatoid) were not collected in the post-sunset period. Although the total number of males of *Odontomachus ruginodis* was greater than the number of females, from November to February more females (207) than males (48) were captured.

Except for *Myrmelachista ramulorum* and *Pheidole moerens*, the other species had more flights in which only one sex was present than both sexes (Table 3). Generally all-male flights were more common than all-female flights. Although flights dominated by males were more common in the fire ant *Solenopsis geminata* and the ponerine *Odontomachus ruginodis* than female dominated flights, these species had a great proportion of nights in which only females were captured.

A total of 71,192 alates corresponding to 14 species were captured in 366 nights during the pre-dawn period (04:00-06:00). Nuptial flights occurred in 83% of the nights. A total of 1,311 flights occurred with an average of 3.6 flights per night (Table 4). *Brachymyrmex heeri* and

Table 4. Number of nuptial flights, listed by sex (Q = queens, M = males) and month, for ant species which flew from 04:00 to 06:00 hours at Guaynabo in 366 nights. Dashes indicate no flights.

Species (Sex)	Oct-99	Nov-99	Dec-99	Jan-00	Feb-00	Mar-00	Apr-00	May-00	Jun-00	Jul-00	Aug-00	Sep-00
Brachymyrmex heeri (Q)	7	5	5	2	5	7	6	16	11	12	11	7
Brachymyrmex heeri (M)	26	20	16	5	7	8	6	16	19	21	30	25
Brachymyrmex obscurior (M)	—	—	—	—	—	—	—	—	—	—	3	1
Hypoponera opacior (Q)	1	—	2	—	—	—	—	1	1	—	1	—
Hypoponera opacior (M)	—	—	1	—	—	—	—	1	2	1	1	—
Pheidole fallax (Q)	4	—	—	—	1	—	1	2	1	—	1	1
Pheidole fallax (M)	21	15	9	—	—	3	9	7	3	8	13	18
Pheidole sculptior (Q)	24	21	12	1	1	1	3	19	16	16	25	24
Pheidole sculptior (M)	28	28	24	4	4	7	8	23	25	26	30	28
Pheidole subarmata (Q)	23	19	9	1	—	—	—	5	10	13	18	18
Pheidole subarmata (M)	27	26	14	2	1	2	1	9	22	23	23	25
Pseudomyrmex simplex (M)	1	—	—	—	—	—	—	—	1	—	1	1
Rogeria foreli (Q)	—	—	—	—	—	—	—	—	1	—	1	—
Rogeria foreli (M)	—	—	—	—	—	—	—	—	2	1	1	—
Solenopsis azteca (Q)	4	3	—	—	—	—	1	3	5	10	5	3
Solenopsis azteca (M)	—	2	2	—	—	—	1	8	13	16	14	10
Solenopsis corticalis (Q)	3	1	2	—	—	2	—	4	5	8	7	4
Solenopsis corticalis (M)	3	—	—	—	—	2	—	—	3	4	—	—
Solenopsis pygmaea (Q)	—	—	—	—	—	—	—	—	1	—	—	—
Tapinoma melanocephalum (Q)	—	—	—	—	—	1	—	—	—	—	—	—
Tapinoma melanocephalum (M)	—	—	—	—	—	—	—	—	—	1	—	1
Wasmannia auropunctata (Q)	15	4	2	—	1	4	9	27	23	25	11	8
Wasmannia auropunctata (M)	9	4	3	—	1	7	20	29	19	7	2	3
Wasmannia sigmoidea (Q)	27	16	7	1	1	1	5	16	21	24	29	27
Wasmannia sigmoidea (M)	31	28	27	10	9	8	14	21	18	28	25	26
Total flights per month[a]	163	130	106	22	24	41	65	126	150	164	167	153
Average flights per night[a]	5.3	4.3	3.4	0.7	0.8	1.4	2.2	4.1	5.0	5.3	5.4	5.1

[a] For all species and a night with both sexes flying counted as one flight.

species of *Wasmannia* and *Pheidole* had the largest flights (Table 5). Species with more than one hundred nuptial flights (Table 6) included the myrmicines: *Wasmannia sigmoidea* (258), *Pheidole sculptior* (242), *Pheidole subarmata* (188), *W. auropunctata* (167), *Pheidole fallax* (107) and the formicine *Brachymyrmex heeri* (204). Apparently stray individuals of the following species, which had flights in the post-sunset period, were collected in the pre-dawn period (Q = queens, M = males): *Camponotus kaura* (2Q:21M), *C. taino* (2M), *Myrmelachista ramulorum*

(9M), *Odontomachus ruginodis* (2M), *Paratrechina myops* (1Q:1M) and *Pheidole moerens* (1Q). As in the post-sunset period most were males.

The data on the 1996 summer nuptial flights (04:00-06:00) were similar to those of 1999-2000, except that males of *Tapinoma melanocephalum* flew more frequently. The males flew on nine occasions (18 males in total) in a period of 66 nights. Also, in two nights a male of *Cyphomyrmex minutus* was captured.

Seasonality was slightly more pronounced in the pre-dawn than in the post-sunset period (Table 4). Most species reduced their activity from January to April (dry season and temperatures in the 16-24.4°C at 06:00 hour). The average number of nuptial flights per night (Table 4) and the total number of alates per month (Fig. 1) were fewer in these months.

Except for *Pheidole sculptior*, *P. subarmata* and *Wasmannia sigmoidea*, the other species had more flights consisting of only one sex than flights

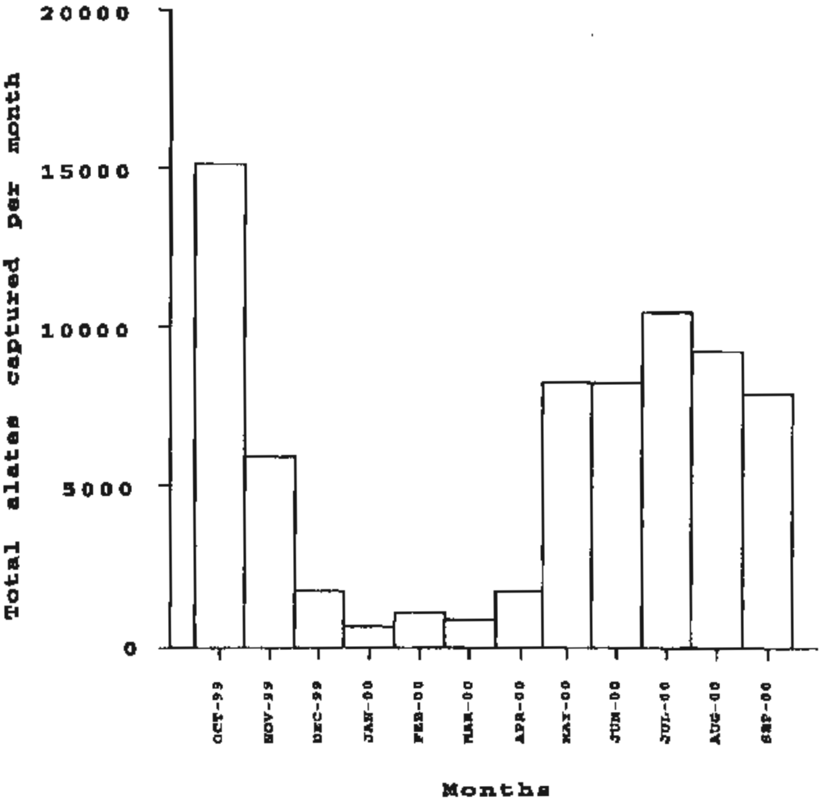

Fig. 1. Total alates in nuptial flights per month at Guaynabo from 04:00-06:00 hours.

Table 5. Frequency of nuptial flights and relative abundance of alates (Q = queens, M = males) trapped at Guaynabo (04:00-06:00 hours) during 366 nights.

Species (sex)	No. of flights	Max. alates in a night	Mean ± SD alates/flight	Total alates
Brachymyrmex heeri (Q)	94	254	12.9 ± 31.2	1208
Brachymyrmex heeri (M)	199	1300	68.8 ± 166.2	13684
Brachymyrmex obscurior (M)	4	1	1.0 ± 0.0	4
Hypoponera opacior (Q)	6	42	8.0 ± 16.7	48
Hypoponera opacior (M)	6	120	21.2 ± 48.4	127
Pheidole fallax (Q)	11	3	1.4 ± 0.8	15
Pheidole fallax (M)	106	368	16.5 ± 51.0	1748
Pheidole sculptior (Q)	163	186	14.1 ± 25.3	2304
Pheidole sculptior (M)	236	1544	51.9 ± 125.2	12258
Pheidole subarmata (Q)	116	167	14.6 ± 24.7	1692
Pheidole subarmata (M)	175	685	44.2 ± 101.8	7735
Pseudomyrmex simplex (M)	4	2	1.3 ± 0.5	5
Rogeria foreli (Q)	2	1	1.0 ± 0.0	2
Rogeria foreli (M)	4	7	3.3 ± 2.9	13
Solenopsis azteca (Q)	34	23	5.1 ± 6.6	173
Solenopsis azteca (M)	66	136	11.2 ± 23.6	742
Solenopsis corticalis (Q)	36	136	9.9 ± 23.1	358
Solenopsis corticalis (M)	12	15	4.0 ± 3.8	48
Solenopsis pygmaea (Q)	1	1	1.0 ± 0.0	1
Tapinoma melanocephalum (Q)	1	1	1.0 ± 0.0	1
Tapinoma melanocephalum (M)	2	1	1.0 ± 0.0	2
Wasmannia auropunctata (Q)	129	741	41.8 ± 117.4	5397
Wasmannia auropunctata (M)	104	1128	27.5 ± 127.1	2856
Wasmannia sigmoidea (Q)	175	479	41.6 ± 70.8	7275
Wasmannia sigmoidea (M)	245	1095	55.1 ± 111.3	13495

with both sexes present (Table 6). All-male flights were more common than flights containing only females in all species, except for *Solenopsis corticalis* and *Wasmannia auropunctata*. In the case of *W. auropunctata* the number of all-female flights was almost identical to those in which both sexes flew together.

As in the post-sunset period the numerical sex ratios were biased in favor of males, except in *Solenopsis corticalis* and *Wasmannia auropunctata* which exhibit an average number of individuals per flight and total number of alates captured biased in favor of females (Table 5). In *W. auropunctata* females dominated the flights from May to October, and males were commoner from November to April (cooler and dry months). Although the total number of males captured in *W. sigmoidea* was greater than females, from June to August more females (3,199) than males (1,377) were captured. We did not capture queens of *Brachymyrmex obscurior* and *Pseudomyrmex simplex* during the predawn period. *Solenopsis pygmaea* males were not captured, nor they

Table 6. Nuptial flights in which only males, only females, or both sexes were trapped from 04:00 to 06:00 hours at Guaynabo in 366 nights. Dashes indicate no flights.

Species	All-male flights	All-female flights	Both sexes	Total flights
Brachymyrmex heeri	110	5	89	204
Brachymyrmex obscurior	4	—	—	4
Hypoponera opacior	4	4	2	10
Pheidole fallax	96	1	10	107
Pheidole sculptior	79	6	157	242
Pheidole subarmata	72	13	103	188
Pseudomyrmex simplex	4	—	—	4
Rogeria foreli	3	1	1	5
Solenopsis azteca	41	9	25	75
Solenopsis corticalis	7	31	5	43
Solenopsis pygmaea	—	1	—	1
Tapinoma melanocephalum	2	1	—	3
Wasmannia auropunctata	38	63	66	167
Wasmannia sigmoidea	83	13	162	258

have been collected in nests.

From 01:00 to 03:00 hours we captured a mixture of individuals belonging to species that had nuptial flights after sunset or before dawn at Guaynabo (Table 7). The total number of flights (all species and at least one sex flying during a night) was 164 in 146 nights for a low average of 1.1 flights per night. The frequency and average size of nuptial flights (Table 7) were smaller than those of the same species flying at their preferred time. Only a total of 1,997 alates were captured, of which 1,837 belonged to *Pheidole subarmata* and *Wasmannia sigmoidea*. These data were collected during the wet season and probably overestimate the frequency and size of flights, which are less frequent and smaller in the dry season. The only species unique to this interval was a queen of *Pyramica membranifera*. Most of the asynchronous individuals flying at this time were males (Table 7), except for *P. subarmata* and *W. sigmoidea*, which suggests that most of these individuals lost their reproductive effort.

We did not find a great deal of separation in time of species belonging to the same genus at Guaynabo. All *Camponotus* species had nuptial flights in the post-sunset period. *Pheidole moerens* flights were in the post-sunset period but the other three species of *Pheidole* had flights during the pre-dawn period. *Solenopsis geminata* had flights in the post sunset period but the three species of *Solenopsis* (*Diplorhoptrum*) had flights during the pre-dawn period. Two species of *Hypoponera* and three of *Paratrechina* had flights in the post-sunset period, while the two

Table 7. Frequency of nuptial flights and relative abundance of alates (Q = queens, M = males) trapped at Guaynabo (01:00 to 03:00 hours) during a period of 146 nights.

Species (sex)	No. of flights	Max. alates in a night	Mean ± SD alates/flight	Total alates
Brachymyrmex heeri (Q)	1	1	1.0 ± 0.0	1
Brachymyrmex heeri (M)	5	21	6.8 ± 8.2	34
Camponotus kaura (Q)	4	1	1.0 ± 0.0	4
Camponotus kaura (M)	14	10	2.4 ± 2.4	33
Camponotus taino (M)	3	2	1.3 ± 0.6	4
Myrmelachista ramulorum (M)	12	5	1.7 ± 1.2	20
Odontomachus ruginodis (M)	3	2	1.3 ± 0.6	4
Paratrechina myops (M)	1	1	1.0 ± 0.0	1
Paratrechina steinhelli (Q)	1	1	1.0 ± 0.0	1
Pheidole moerens (Q)	3	1	1.0 ± 0.0	3
Pheidole moerens (M)	4	21	10.0 ± 8.3	40
Pheidole sculptior (Q)	5	1	1.0 ± 0.0	5
Pheidole sculptior (M)	3	3	1.7 ± 1.2	5
Pheidole subarmata (Q)	36	40	6.9 ± 8.6	249
Pheidole subarmata (M)	51	178	14.6 ± 30.3	742
Pyramica membranifera (Q)	1	1	1.0 ± 0.0	1
Solenopsis corticalis (Q)	1	1	1.0 ± 0.0	1
Solenopsis corticalis (M)	1	1	1.0 ± 0.0	1
Wasmannia auropunctata (Q)	1	1	1.0 ± 0.0	1
Wasmannia auropunctata (M)	1	1	1.0 ± 0.0	1
Wasmannia sigmoidea (Q)	16	11	3.0 ± 3.4	48
Wasmannia sigmoidea (M)	47	184	17.0 ± 39.0	798

species of *Wasmannia* had flights during the pre-dawn period. Not only species in the same genus usually had flights during the same time period in a night, but also on similar dates during the year.

At the Guánica dry forest we captured a total of 16,483 alates in 620 nights (Table 8a,b). Nuptial flights occurred in 75% of the nights. There were 1,315 nuptial flights (all species and at least one sex flying during a night) for an average of 2.1 flights per night. Species with more than one hundred nuptial flights included the myrmicines *Crematogaster steinheili* (193), *Cyphomyrmex minutus* (126) and *Solenopsis torresi* (107); the formicines *Camponotus kaura* (143) and *Brachymyrmex heeri* (113); and the ponerine *Odontomachus ruginodis* (108).

As in the Guaynabo site, at Guánica the number of flights was fewer during the dry season. Flights tended to be less frequent from the months of December to June (Table 8a,b). The year 1996 was wetter (697 mm of rain) compared to 1997 (420 mm). In 1996 the dry season was shorter, and that could explain the large number of flights in June 1996 (106 mm of rain) compared to June 1997 (3 mm of rainfall). The seasonality was more pronounced in the females: not a single female

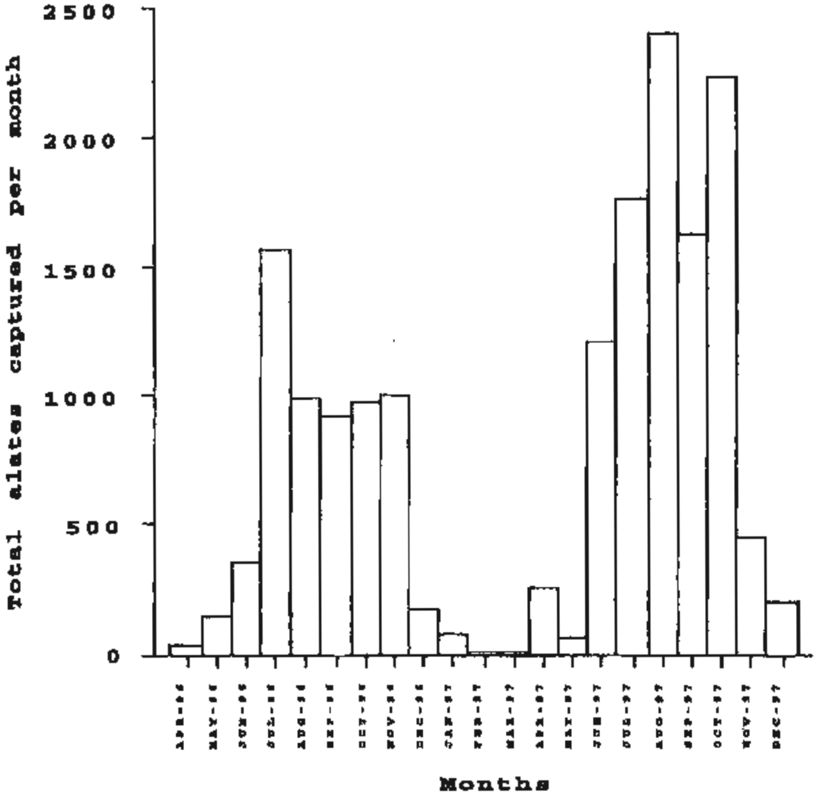

Fig. 2. Total alates in nuptial flights per month at the Guánica dry forest from August 1996-December 1997

of any species was captured in February and March. The total number of alates captured per month was fewer during the same months, except in June 1997 (Fig. 2). The high total number of alates in June 1997 was due to the occurrence of a large flight of *Crematogaster steinhelli* that accounted for 93% of the alates captured during the whole month. Most species had nuptial flights during the same dates with little differentiation among species (Table 8a,b). Species with a high frequency of nuptial flights at Guaynabo (e.g., *Camponotus sexguttatus*, *Myrmelachista ramulorum*, *Pheidole subarmata*, *Solenopsis geminata* and *Wasmannia auropunctata*) were rarely seen flying at Guánica. On the other hand, flights of *Cyphomyrmex minutus* were common at Guánica, but rare at Guaynabo.

Although the Guánica data on nuptial flights refer to the entire night, the total and average number of flights per night were fewer (Table 8a,b)

Table 8a. Number of ant nuptial flights, listed by sex (Q = queens, M = males) and month, at Guánica forest in 1996 (N = 261 nights). Dashes indicate no flights.

Species (sex)	Apr-96	May-96	Jun-96	Jul-96	Aug-96	Sep-96	Oct-96	Nov-96	Dec-96
Amblyopone sp. (M)	—	—	1	—	1	—	—	1	1
Anochetus kempfi (M)	2	1	8	7	8	2	7	3	2
Brachymyrmex heeri (Q)	—	—	—	1	3	1	1	5	1
Brachymyrmex heeri (M)	—	2	3	4	8	9	12	13	10
Brachymyrmex obscurior (M)	—	—	—	1	—	—	—	—	—
Camponotus kaura (Q)	—	—	—	6	1	—	1	—	—
Camponotus kaura (M)	1	1	7	16	16	11	11	—	—
Cramatogaster steinheili (Q)	—	3	7	9	10	11	8	5	1
Crematogaster steinheili (M)	—	2	6	14	15	18	11	11	7
Cyphomyrmex minutus (Q)	—	—	—	—	1	—	—	1	—
Cyphomyrmex minutus (M)	3	7	9	11	19	15	11	10	4
Dorymyrmex sp. (M)	—	—	2	3	—	—	1	1	—
Hypoponera opacior (Q)	—	—	—	—	—	1	1	—	1
Leptogenys pubiceps (M)	—	—	—	1	2	1	2	1	—
Leptothorax torrei (M)	—	2	1	—	12	8	—	5	—
Monomorium ebeninum (M)	—	2	—	—	1	—	—	—	—
Monomorium floricola (M)	—	—	—	—	—	—	—	1	—
Myrmelachista ramulorum (Q)	—	—	2	—	—	1	—	—	—
Myrmelachista ramulorum (M)	1	1	2	—	3	1	—	1	—
Odontomachus ruginodis (Q)	—	5	2	1	—	1	—	1	—
Odontomachus ruginodis (M)	—	2	11	12	12	5	13	3	3
Paratrachina longicornis (M)	1	6	2	4	5	5	9	5	2
Paratrachina myops (M)	—	—	—	—	1	—	—	—	—
Paratrechina steinheili (Q)	1	—	—	—	—	—	—	—	—
Paratrechina steinheili (M)	—	—	—	—	1	2	—	—	1
Pheidole spp. (Q)	—	—	1	1	2	—	3	—	1
Pheidole spp. (M)	2	5	3	1	2	1	6	2	1
Pheidole subarmata (Q)	—	—	—	—	—	—	1	—	—
Probolomyrmex sp. (M)	—	—	3	2	8	4	3	3	4
Pseudomyrmex simplex (M)	—	1	2	1	4	3	2	1	1
Rogeria carinata (M)	—	—	1	—	—	—	1	—	—
Solenopsis geminata (Q)	—	—	—	—	—	1	—	—	1
Solenopsis geminata (M)	1	—	1	—	—	1	1	2	—
Solenopsis globularia (Q)	—	—	1	2	—	1	2	—	—
Solenopsis globularia (M)	2	—	4	13	8	3	11	4	4
Solenopsis torresi (Q)	—	1	3	4	22	9	8	1	3
Solenopsis torresi (M)	—	—	1	1	6	8	5	—	—
Technomyrmex albipes (M)	—	—	—	—	—	—	—	1	—
Tetramorium bicarinatum (M)	—	—	—	—	—	—	1	—	—
Tetramorium caldarium (Q)	—	—	1	2	3	—	—	—	—
Trachymyrmex jamaicensis (M)	—	—	—	—	—	—	1	3	—
Wasmannia auropunctata (Q)	—	—	—	—	—	1	—	—	—
Total flights per month[a]	15	39	76	100	159	104	121	76	47
Average flights per nights[a]	0.7	1.3	2.5	3.3	5.1	4.3	3.9	2.5	1.5

[a] For all species and a night with both sexes flying counted as one flight.

Table 8b. Number of ant nuptial flights, tabulated by sex (Q = queens, M = males) and month, at Guánica forest in 1997 (N = 359 nights). Dashes indicate no flights.

Species (sex)	Jan-97	Feb-97	Mar-97	Apr-97	May-97	Jun-97	Jul-97	Aug-97	Sep-97	Oct-97	Nov-97	Dec-97
Amblyopone sp. (M)	—	—	—	—	—	—	—	—	—	—	—	1
Anochetus kempfi (M)	2	1	—	1	7	3	6	6	3	5	2	—
Brachymyrmex heeri (Q)	1	—	—	2	—	—	—	—	3	8	—	—
Brachymyrmex heeri (M)	4	—	1	5	1	—	7	2	7	16	5	1
Brachymyrmex obscurior (M)	—	—	—	—	—	—	—	—	1	1	—	—
Camponotus kaura (Q)	—	—	—	—	—	—	—	3	2	—	2	—
Camponotus kaura (M)	1	—	—	2	—	7	19	22	13	8	4	3
Camponotus sexguttatus (Q)	—	—	—	—	—	—	1	—	—	—	—	—
Crematogaster steinheili (Q)	—	—	—	1	4	3	11	9	8	9	4	3
Crematogaster steinheili (M)	5	—	2	—	4	4	14	11	13	12	11	8
Cyphomyrmex minutus (Q)	—	—	—	—	—	—	1	—	2	1	2	1
Cyphomyrmex minutus (M)	6	—	—	1	—	—	2	—	4	6	12	5
Dorymyrmex sp. (M)	—	—	—	—	—	—	1	—	—	—	—	1
Hypoponera opaciceps (Q)	—	—	—	—	—	—	—	—	—	—	—	1
Hypoponera opacior (Q)	—	—	—	1	—	—	—	—	—	—	—	—
Leptogenys pubiceps (M)	1	—	—	—	1	3	—	—	1	—	1	—
Leptothorax torrei (M)	1	3	5	5	3	9	4	2	1	4	1	—
Myrmelachista ramulorum (Q)	—	—	—	—	—	1	—	1	—	1	—	—
Myrmelachista ramulorum (M)	—	—	—	3	4	4	4	2	1	2	—	2
Odontomachus ruginodis (Q)	1	—	—	—	—	—	1	—	—	—	—	1
Odontomachus ruginodis (M)	—	3	1	—	6	8	4	3	5	2	4	2
Paratrechina longicornis (M)	1	—	—	1	—	2	5	1	—	3	3	2
Pheidole fallax (M)	—	—	—	—	—	—	—	—	—	—	1	—
Pheidole spp. (Q)	—	—	—	—	—	—	—	1	—	—	—	—
Pheidole spp. (M)	1	—	—	—	—	—	1	—	—	—	—	—
Probolomyrmex sp. (M)	2	1	—	—	—	—	—	—	—	—	1	—
Pseudomyrmex simplex (M)	1	—	—	—	—	—	1	—	1	1	—	—
Rogeria carinata (M)	—	—	—	—	—	—	—	—	—	1	—	—
Solenopsis geminata (Q)	—	—	—	—	—	—	—	—	—	—	1	5
Solenopsis geminata (M)	—	—	—	—	—	—	—	1	1	—	—	2
Solenopsis globularia (Q)	—	—	—	1	—	—	1	1	1	1	1	—
Solenopsis globularia (M)	—	—	—	1	2	5	6	4	7	1	8	8
Solenopsis torresi (Q)	—	—	—	—	—	1	1	2	10	6	6	3
Solenopsis torresi (M)	1	—	—	—	—	—	—	2	6	6	12	12
Technomyrmex albipes (M)	—	—	—	—	—	—	—	—	1	—	—	—
Tetramorium bicarinatum (Q)	—	—	—	—	—	1	—	—	—	—	—	—
Tetramorium bicarinatum (M)	—	—	—	—	—	—	—	—	1	—	—	—
Tetramorium caldarium (Q)	—	—	—	1	—	—	—	—	—	3	1	1
Tetramorium caldarium (M)	—	—	—	—	—	—	—	—	—	1	—	—
Trachymyrmex jamaicensis (M)	—	—	—	—	—	—	—	—	—	2	1	—
Wasmannia auropunctata (Q)	—	—	—	—	—	—	1	—	—	—	—	—
Total flights per month[a]	27	8	9	23	30	47	82	63	74	80	77	58
Average flights per night[a]	0.9	0.3	0.3	0.8	0.9	1.6	2.6	2.1	2.5	2.6	2.6	2.2

[a] For all species and a night with both sexes flying counted as one flight.

Table 9. Frequency of nuptial flights and relative abundance of alates (Q = Queens, M = Males) trapped (listed by sex) at Guánica dry forest in 620 nights.

Species (sex)	No. of flights	Max. alates in a night	Mean ± SD alates/flight	Total alates
Amblyopone sp. (M)	5	1	1.0 ± 0.0	5
Anochetus kempfi (M)	76	4	1.2 ± 0.5	90
Brachymyrmex heeri (Q)	26	53	4.8 ± 10.3	124
Brachymyrmex heeri (M)	110	203	26.0 ± 38.0	2855
Brachymyrmex obscurior (M)	3	2	1.3 ± 0.6	4
Camponotus kaura (Q)	15	10	2.5 + 2.8	38
Camponotus kaura (M)	142	265	8.0 ± 30.0	1137
Camponotus sexguttatus (Q)	1	4	4.0 ± 0.0	4
Crematogaster steinheili (Q)	106	583	33.6 ± 97.7	3562
Crematogaster steinheili (M)	168	614	37.0 ± 102.0	6222
Cyphomyrmex minutus (Q)	9	2	1.3 ± 0.5	12
Cyphomyrmex minutus (M)	125	83	6.8 ± 10.7	853
Dorymyrmex sp. (M)	9	3	1.4 ± 0.7	13
Hypoponera opaciceps (Q)	1	1	1.0 ± 0.0	1
Hypoponera opacior (Q)	4	1	1.0 ± 0.0	4
Leptogenys pubiceps (M)	14	1	1.0 ± 0.0	14
Leptothorax torrei (M)	66	120	3.6 ± 14.6	236
Monomorium ebeninum (M)	3	8	3.3 ± 4.0	10
Monomorium floricola (M)	1	1	1.0 ± 0.0	1
Myrmelachista ramulorum (Q)	6	5	1.7 ± 1.6	10
Myrmelachista ramulorum (M)	31	17	2.5 ± 3.1	78
Odontomachus ruginodis (Q)	13	7	1.6 ± 1.7	21
Odontomachus ruginodis (M)	99	21	1.9 ± 2.5	192
Paratrechina longicornis (M)	57	22	3.6 ± 5.2	206
Paratrechina myops (M)	1	1	1.0 ± 0.0	1
Paratrechina steinheili (Q)	1	1	1.0 ± 0.0	1
Paratrechina steinheili (M)	4	3	2.0 ± 1.2	8
Pheidole fallax (M)	1	1	1.0 ± 0.0	1
Pheidole spp. (Q)	9	5	1.9 ± 1.8	17
Pheidole spp. (M)	25	30	3.0 ± 5.8	76
Pheidole subarmata (Q)	1	1	1.0 ± 0.0	1
Probolomyrmex sp. (M)	31	3	1.1 ± 0.5	35
Pseudomyrmex simplex (M)	19	1	1.0 ± 0.0	19
Rogeria carinata (M)	3	1	1.0 ± 0.0	3
Solenopsis geminata (Q)	8	17	4.3 ± 5.5	34
Solenopsis geminata (M)	10	1	1.0 ± 0.0	10
Solenopsis globularia (Q)	12	1	1.0 ± 0.0	12
Solenopsis globularia (M)	91	6	1.5 ± 1.0	136
Solenopsis torresi (Q)	80	9	1.9 ± 1.6	153
Solenopsis torresi (M)	58	23	4.0 ± 4.5	230
Tapinoma melanocephalum (M)	19	3	1.1 ± 0.5	21
Technomyrmex albipes (M)	2	1	1.0 ± 0.0	2
Tetramorium bicarinatum (Q)	1	1	1.0 ± 0.0	1
Tetramorium bicarinatum (M)	2	1	1.0 ± 0.0	2
Tetramorium caldarium (Q)	12	3	1.3 ± 0.7	16
Tetramorium caldarium (M)	1	1	1.0 ± 0.0	1
Trachymyrmex jamaicensis (M)	7	3	1.3 ± 0.8	9
Wasmannia auropunctata (Q)	2	1	1.0 ± 0.0	2

Table 10. Nuptial flights in which only males, only females, or both sexes were trapped at Guánica dry forest in 620 nights. Dashes indicate no flights.

Species	All-male flights	All-female flights	Both sexes	Total flights
Amblyopone sp.	5	—	—	5
Anochetus kempfi	76	—	—	76
Brachymyrmex heeri	87	3	23	113
Brachymyrmex obscurior	3	—	—	3
Camponotus kaura	128	1	14	143
Camponotus sexguttatus	—	1	—	1
Crematogaster steinheili	87	25	81	193
Cyphomyrmex minutus	117	1	8	126
Dorymyrmex sp.	9	—	—	9
Hypoponera opaciceps	—	1	—	1
Hypoponera opacior	—	4	—	4
Leptogenys pubiceps	14	—	—	14
Leptothorax torrei	66	—	—	66
Monomorium ebeninum	3	—	—	3
Monomorium floricola	1	—	—	1
Myrmelachista ramulorum	28	3	3	34
Odontomachus ruginodis	95	9	4	108
Paratrechina longicornis	57	—	—	57
Paratrechina myops	1	—	—	1
Paratrechina steinheili	4	1	—	5
Pheidole fallax	1	—	—	1
Pheidole spp.	21	4	5	30
Pheidole subarmata	—	1	—	1
Probolomyrmex sp.	31	—	—	31
Pseudomyrmex simplex	19	—	—	19
Rogeria carinata	3	—	—	3
Solenopsis geminata	9	7	1	17
Solenopsis globularis	85	6	6	97
Solenopsis torresi	27	49	31	107
Tapinoma melanocephalum	19	—	—	19
Technomyrmex albipes	2	—	—	2
Tetramorium bicarinatum	2	1	—	3
Tetramorium caldarium	—	11	1	12
Trachymyrmex jamaicensis	7	—	—	7
Wasmannia auropunctata	—	2	—	2

than those from the post-sunset and pre-dawn periods at Guaynabo. Also, the proportion of nights in which the different species had flights at Guánica tended to be fewer than in the post-sunset and pre-dawn periods at Guaynabo. In addition, the 16,483 alates captured in 620 nights was low compared to 18,607 alates captured in 92 nights in the post-sunset period at Guaynabo and 71,192 in 366 nights in the pre-dawn period at Guaynabo.

Also, at the Guánica forest most species had numerical sex ratios biased in favor of males (Table 9). In eighteen species (Table 9) we did not capture females (*Anochetus kempfi*, *Monomorium ebeninum* and *M. floricola* have ergatoid queens that do not fly). In *Leptogenys pubiceps* probably queens are ergatoid or the queen caste has been replaced by egg-laying workers (Wheeler 1910, Davies *et al.* 1994). In *Crematogaster steinhelli*, although total males were more abundant than queens, queens were more common in May 1996, 1997, June 1996 and July 1997. During the months of June and August 1997 queens and males were captured in almost equal proportions. Also, in *Solenopsis torresi* more males were captured but queens were captured in greater numbers in 10 months and males dominated in only six months. As at Guaynabo there were more nights in which one sex flew than both (Table 10).

The variance (Tables 2, 5 and 9, the square of the SD) in the number of males flying tended to be greater (with few exceptions) than in females of the same species even though is based on a greater sample size (males generally flew on a greater number of nights).

When the meteorological conditions were favorable, most species had nuptial flights. We found that many flights were associated with rains, especially if there have been several days without rain; but once the rainy season began flights occurred independent of the presence of rains. Flights at both sites occurred with more frequency during the rainy season. It was unusual to have a flight while rain was falling, but we observed this at Guaynabo on three occasions. We did not observe nuptial flights when wind speed was above 40 km/hr.

DISCUSSION

Two of the most notable findings of this study were the high frequency of nuptial flights of some species and the low seasonality of flights, especially in moist habitats like the Guaynabo site. At Guaynabo, in the post-sunset period nuptial flights occurred in 96.4% of the nights. If we add those flights that occurred in the pre-dawn period and the flights of species that have flights during the day, we can conclude that at least one nuptial flight occurred every day. Probably a high frequency of flights is a common phenomenon in tropical ant species. Kempf (1963) found mating flights of *Mycocepurus goeldii* from October to February in Brazil. Nuptial flights of fire ants (*Solenopsis wagneri* and *S. richteri*) have been noted every month in the USA (Markin *et al.* 1971), which could be related to the tropical origin of these species. Leston (1979) found males of army ant species (Dorylini) flying throughout the year, with a peak in the wet sunny season. As in this study, Leston found that flights of doryline, formicine, myrmicine and ponerine ants were concurrent. In addition, Haddow *et al.* (1966) found that male driver ants fly throughout the year in Uganda and seasonal fluctuations in abundance are probably not much greater than the night to night variations. On the other hand, flights of New World army ant males are more seasonal and occur during the dry season and early rainy season (Kannowski 1969, Baldrige *et al.* 1980). It appears that notions about the infrequency of ant nuptial flights (Bourke & Franks 1995) based on studies of a few temperate species may be incorrect.

A great proportion of the species had nuptial flights during the night. Nocturnal flights could be a behavior to avoid diurnal predators and desiccation. Also, crepuscular hours are less windy than daylight hours and more favorable for swarming by small insects (Sullivan 1981). Contrary to Kannowski (1969) and Baldridge *et al.* (1980), we did not observe any association between phases of the moon and nuptial flight activity.

Numerical male biased sex ratio in nuptial flights was frequent, but some species exhibited female biased sex ratios in this study. Male bias in the numerical sex ratio seems a frequent occurrence in ants (Kannowsky 1969, Bourke & Franks. 1995), and males are more abundant in flights of several species (Tarpley 1965, Markin *et al.* 1971, Kannowski 1972, Elmes & Webb 1985, Woyciechowski 1990). However, predominantly female swarms have been observed in *Acropyga* in Colombia (Eberhard 1978) and in a species of *Pheidole* in New Zealand (Little 1980).

Species in which the total males captured were greater than females had some flights in which females predominated or in which only females flew. Also, there was a great proportion of flights in which only one sex flew. Even when both sexes flew, generally there was an excess of males. Male abundance in flights was more variable than that of females, even though they flew on more nights. A lot of the investment in ant reproduction seems to be lost due to lack of synchronization (in time and numbers) in ant nuptial flights. Perhaps the great number of male flights and the large variance in abundance per flight are the result of a bet-hedging strategy (Stearns 1976), because it is difficult for males to predict with certainty when the females are going to fly. Similarly optimal allocation in sex ratio was not observed in *Linepithema humile* (Keller & Passera 1992). Production of males occurs before that of females and lasts longer than female production. Also, the last males may emerge when there are no females in the colony. Also, Yamauchi *et al.* (1986) have found late summer flights in *Lasius* that consist of only males.

Models to predict the fitness payoffs from producing a certain number of sexuals show that the fitness payoffs are functions of the sex ratio (Bourke & Franks 1995, Crozier & Pamilo 1996). Specifically the fitness payoff is calculated as the product of (number of offspring of one sex X the regression relatedness X sex-specific reproductive value X mating success). Many of these models calculate mating success as the reciprocal of the abundance of each sex. As found in this study, mating success is a complex function which cannot be determined by only examining or counting sexuals in nests. In terms of numerical sex ratio we need to distinguish between passive sex ratio (as estimated from nest censuses) and the effective sex ratio as found in a swarm to establish the mating success of individuals.

We found that ant species at Guaynabo fall into two groups: the post-sunset and the pre-dawn. Probably this is a common phenomenon in ants. It has been observed in male army ants (Kannowsky 1969) and in some species of *Leptothorax* (Plateaux 1987). McCluskey (1963) found that a light-phase relationship is valuable in synchronizing nuptial flights and probably the changes in light intensity associated with sunset and dawn is the stimulus that help synchronize these flights.

There were no species specialized to fly in the middle of the night. Although there can be selection to have flights at different times to avoid interspecific matings, other factors can promote synchronization of nuptial flights of different species. Predator avoidance will be greater the larger the number of alates flying independent of the species identities. Also, the external cues that ants need to synchronize their flights could be limited. Great overlap in other niche dimensions have been observed on these ants in Puerto Rico (Torres 1984).

As shown in this study, species of *Atta* and *Mycocepurus* tend to swarm simultaneously (Kerr 1961, Kempf 1963, Amante 1972, Weber 1972). Interbreeding has not been observed in these flights. Species of *Neivamyrmex* have similar male flight seasons and there is no evidence that flight season facilitates sexual isolation (Baldridge *et al.* 1980). Some species of *Pogonomyrmex* and *Myrmica* could fly at the same time, but interspecific copulations have been reported (Collingwood 1958, Nagel & Rettenmeyer 1973). Yamauchi *et al.* (1986) found that most nuptial flights in *Lasius* occur in a rather short period of time in the early morning or in the evening. Species of *Lasius* differ in the season and time of the day when nuptial flights take place and opportunities for hybridization are very low.

It has been suggested that nuptial flights help dispersal of ants (Nagel & Rettenmeyer 1973) but this does not seem to be common. We found that most species did not fly when there were strong winds, which is the best time for long distance dispersal. Similarly, strong winds prevent nuptial flights in *Atta texana* (Moser 1967) and in *Neivamyrmex* males (Baldridge *et al.* 1980). Yamauchi *et al.* (1986) found that wind so weak as to only slightly wave nearby herbs was sufficient to stop flights in *Lasius* spp. Even in *Solenopsis wagneri*, in which wind assisted dispersal has been documented, most flights occur when wind velocity is less than 8km/hr (Markin *et al.* 1971). Many insects are apparently unable to conduct their usual movements when flying in a wind (Sullivan 1981). Strong winds could interfere with swarm formation and mating.

Members of the following ant subfamilies are present in Puerto Rico: Ponerinae, Cerapachyinae (one rare species), Pseudomyrmecinae, Myrmicinae, Dolichoderinae and Formicinae. All subfamilies, except the Dolichoderinae and Cerapachyinae, include species in which nuptial flights occurred with a high frequency. More research is needed in the Dolichoderinae in other areas to see if this is a general characteristic of this subfamily.

Wasmannia auropunctata had a high frequency of nuptial flights at Guaynabo. This species has a patchy distribution with areas of local high dominance, but is rare in the islands surrounding Puerto Rico (Torres & Snelling 1997). Although *W. auropunctata* had a high frequency of nuptial flights, probably after mating they fly only for short distances (Levins *et al.* 1973) which could explain its restricted distribution.

Rogeria foreli was captured in low numbers at Guaynabo during the pre-dawn period; but it seems to be more active during the day, as found by our collections using Malaise traps operating during the day. Also, we have captured *Rogeria carinata* frequently in a Malaise trap operating 24 hours a day at the Guánica forest, which indicates that this species probably starts flying during the pre-dawn period but extends its flying period to the early morning hours. Apparently *Brachymyrmex obscurior* also prefers to fly during the day. We did not capture females in the light traps, but we have captured *B. obscurior* females in Malaise traps.

There are several species that exhibit unusual flight patterns, and in some additional research is needed to explain these patterns. Only one queen of *Tapinoma melanocephalum* was captured. In *T. melanocephalum* mating can occur inside the nests (Levins *et al.* 1973), and that could explain the low queen number. Males of *Solenopsis corticalis* appeared in low numbers compared to queens. We have observed flights of *S. corticalis* after sunrise and males during daytime hours were more abundant than queens. It is possible that queens start flying earlier than males, and that could explain the low number of males in the pre-dawn period.

Males of a species of *Probolomyrmex* were captured with great frequency in 1996 at the Guánica dry forest, but were rare in 1997. Maybe the low rainfall in 1997 affected this subterranean species. We have not been able to find workers or queens of this species. In *Leptothorax torrei* we captured great numbers of males, but no females. We have found queens of this species only by sifting leaf litter. The biology of this species needs to be studied to see what happens to the queens. Queens of *Pseudomyrmex simplex*, *Dorymyrmex* sp. (we have collected alate queens in nests) and *Amblyopone* sp. were not captured. Research is needed to see if females in these species have abandoned nuptial flights or if they continue their nuptial flights during the day. Males of *Tetramorium* were rarely captured and more information is needed to see if they concentrate their flights during the day.

The following species have ergatoid queens: *Monomorium ebeninum*, *M. floricola* and *Anochetus kempfi*. Males of *Monomorium* were rarely captured, but males of the ponerine *Anochetus kempfi* (a nocturnal species, Torres *et al.* 2000) were captured with relatively high frequency. Workers of both species of *Monomorium* are diurnal (Torres 1984), and males probably prefer to have nuptial flights during the day.

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