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SEASONAL OCCURRENCE OF FOUNDING QUEENS AND THE SEX RATIO OF *CAMPONOTUS PENNSYLVANICUS* (HYMENOPTERA: FORMICIDAE) IN NEW JERSEY

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Abstract.—Founding queens of *Camponotus pennsylvanicus* were collected in the field from early March through the middle of July from 1977 to 1981. No synchronization of population nuptial flights was detected. Sex ratios of colonies are male biased, contrary to previous reports.

The carpenter ant, *Camponotus pennsylvanicus* (DeGeer), is one of the most ubiquitous of all urban insects in the Northeast. As early as 1910, Wheeler reported on its synanthropic adaptations, and, if anything, this relationship has grown as urbanization has progressed. In spite of this fact, our knowledge of its biology has not notably improved since Pricer (1908) published his detailed studies. McCook (1883a, b), Blochmann (1885), and Pricer (1908) have described the initiation of an incipient colony by founding queens. Here, we describe the seasonal distribution of the nuptial flights, and the sex ratio of field colonies, both of which are important to understanding the reproductive strategy of this insect. We also discuss the implications of our observations on the organization of its population structure.

Methods

The data we report on here is largely field data that we have collected from 1977 to 1981, on the captures of alate or recently dealated queens of *C. pennsylvanicus* in central New Jersey. However, the data from 1979 is derived from student collections, as we were unable to collect during that year.

Sex ratio information was taken from colonies collected in their entirety in early spring, employing a modification of Vanderschaff's (1970) method. In all cases, colonies were collected before the mode of occurrences of nuptial flights, as inferred from our field data. Dry weights were determined for 30 males and females, and were used for subsequent interpretations.

Statistical tests employed here are of goodness of fit of distributions: the Kolmogrov-Smirnov test statistic, D; and the Log-Likehood Ratio test statistic, G (Zar 1974).

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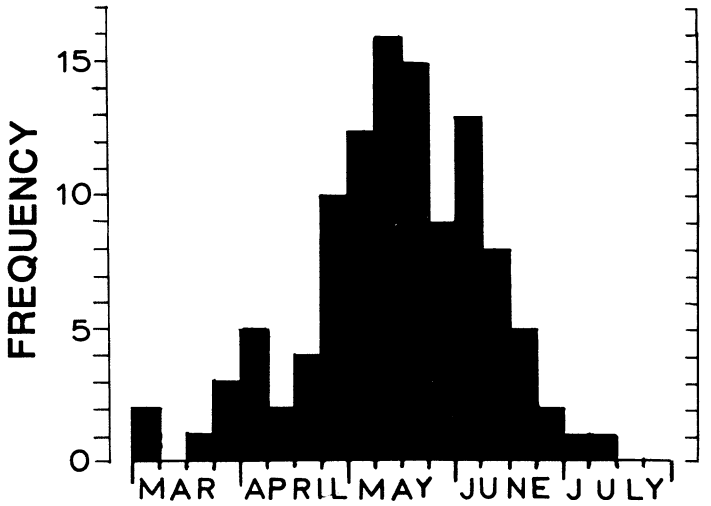

Fig. 1. The distribution of field collections of alate or recently dealate queens of *C. pennsylvanicus* from 1977 through 1981, in central New Jersey.

Results

A plot of the data of the occurrences of field captures of alate or recently dealate *C. pennsylvanicus* queens (Fig. 1) demonstrates that most nuptial flights occurred during spring. Surprisingly, founding queens were captured for more than four months (Fig. 1).

If we compare the data collection on an annual basis (Table 1), we find that we cannot reject the null hypothesis that there is significant variation in the numbers of queens captured (Kolmogrov-Smirnov $D = 0.12615$, $P > 0.05$), but we must conclude that there is a significant seasonal, or monthly,

Table 1. The monthly and yearly distributions of collections of alate or recently dealate queens of *C. pennsylvanicus* given in Fig. 1.

Month	Year					
	1977	1978	1979*	1980	1981	Sum
March	0	1	0	1	4	5
April	3	9	0	4	7	23
May	6	18	8	15	6	53
June	5	9	4	8	2	28
July	0	0	0	2	0	2
Sum	14	37	12	29	19	111

* All data from student collections.

Table 2. The sex ratios of reproductives from New Jersey field colonies of *C. pennsylvanicus*, and a comparison with data given in Pricer (1908).

Colony reference number	Alates collected		Proportion males
Pricer #1	350		0.4286
Pricer #2	370		0.4708
Pricer #3	323		0.3591
Pricer #4	206		0.4951
Total	1,249	Mean ratio	0.4339
New Jersey colonies collected in spring 1980			
Queens present			
CP #32	526		0.6026
CP #39	410		0.4805
CP #40	1,009		0.5154
CP #42	1,120		0.6151
CP #45	260		0.4846
Total	3,325	Mean ratio	0.5561
Queens not recovered			
CP #37	75		0.7600
CP #38	217		0.4746
CP #41	437		1.0000
Total	729	Mean ratio	0.8189

effect on capture distributions (Kolmogrov-Smirnov $D = 0.181982$, $P < 0.0002$).

Field collected colonies of *C. pennsylvanicus* also were variable in sex ratio (Table 2). The mean ratio of males to females was 1.516, or 60.26% of all reproductives in the colonies were males. However, if we compare those colonies from which queens were not recovered with queenright colonies, we find that queenless colonies have a significantly higher frequency of males (0.81893 vs. 0.55188; $G = 189.579$, $P < 0.00001$). Also, our colonies collected in New Jersey had a significantly higher frequency of males than did Pricer's (1908) colonies (0.6026 vs. 0.4339; $G = 109.74$, $P < 0.00001$). Mean dry weight of female alates was 56.8 ± SD 12.3 mg, while that of the males was 9.3 ± SD 4.3 mg. Assuming equivalence in conversion costs, a female is thus 6.1 times more costly to produce than a male.

Discussion

Direct observations of synchronous mass mating swarms of *Camponotus* spp. have not been recorded. Males produce a mandibular gland pheromone which stimulates the females to flight (Holldobler and Maschwitz 1965). However, Veitinghoff-Riesch (1928) and Sanders (1972) have provided indi-

rect evidence that synchronous swarming may occur in *C. herculeanus* (L.). Typically, alates depart from the colony individually, and ascend until they are no longer visible, presumably to mate in the air (Eidmann 1929; Sanders 1964).

The data that we have been able to collect does not suggest synchronous swarming of *C. pennsylvanicus* in New Jersey. Moreover, our data suggest that nuptial flights occur over a very long period of time, and generally involve a limited number of queens. Our data do not allow a consideration of the temporal range of the mating activities of males, but we assume that it must be similar. The distribution of our capture data does not differ significantly from carpenter ant complaints from the general public in New Jersey (Fowler and Roberts 1982), suggesting that the general public may respond to sightings of individual founding queens.

Trivers and Hare (1976) have extended the argument of sex ratio and incorporated it with the theory of kin-selection to argue that monogynous ants, such as *C. pennsylvanicus,* should have a sex ratio controlled by the workers. If so, the sex ratio should approximate 1 male to 3 females, on a per weight basis, given the asymmetries of genetic relatedness. A recalculation of Trivers and Hare's (1976) data for *C. pennsylvanicus,* based on a larger sample size for dry weight determinations, gives an inverse ratio of investment, of the weight ratio of females to males divided by the ratio of the number of males to females, of 7.92 for Pricer's (1908) data. For our data from New Jersey, this ratio is 4.07. If we examine the data from queenright and queenless colonies separately, we find an inverse ratio of investment of 5.8 for queenright colonies and 1.35 for queenless colonies. Only when a queen has died, or is lost, as was probably the case in our queenless colonies, does this ratio drop, as would be expected, under worker oviposition leading to increased production of males. As the ratio of investment was highly variable from colony to colony, it is likely that there is no optimum ratio of investment, as has been argued by Herbers (1979) and Cannings and Cruz Orive (1975).

If we consider an elementary model of sex ratio investment (Cannings and Cruz Orive 1975), in which the more abundant sex is shown to be the disperser, we may conclude that alate queens do not widely disperse, but rather males must if outbreeding is to occur. Isozyme studies of localized populations are needed to test this prediction.

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