THE ORGANIZATION OF A NUPTIAL FLIGHT OF THE ANT *PHEIDOLE SITARCHES* WHEELER

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Introduction. Most published information on the sexual behavior of ants relates solely to the inception of the nuptial flights, with very little being recorded of the behavior of the individual reproductive forms during the main part of the flights. The reason for this important gap in our knowledge is plain — in the great majority of ant species the reproductives scatter widely after leaving the nest, fly moderate to long distances, and finally mate in nuptial swarms far above the head of the human observer.

The nuptial flight is of more than ordinary interest to the student of social insects. It is here that the male ants exhibit, both in the formation and maintenance of the swarms and in subsequent copulatory movements, the greater part of their lifetime social behavior. Both sexes display fixed-action patterns, conceivably complex in nature, that appear only at this time and are apt to be among the most stereotyped and species-specific of the entire species' repertory. Judging from other animal groups in which the reproductive behavior is better known, the nuptial flight patterns of ants can be expected to have at least four essential adaptive features, which can be summarized as follows: synchronization and coordination of flight movements within the species, intraspecific sexual stimulation to copulatory levels, exclusion of other species from the final swarming and copulatory activity, and regulation of the species dispersal rate. Descriptions of nuptial flight behavior should include, among other things, information bearing on these topics.

Observations. During field work in New Mexico in the summer of 1952, the author had an unusual opportunity

to observe a nuptial flight of the small myrmicine ant *Pheidole sitarches*. The flight occurred on August 9 near Datil, Catron Co., in an abandoned homesite surrounded by sparse juniper woods. The area, normally very dry, had received a moderate rain during the afternoon, so that the upper layers of soil were moistened, and in the late afternoon, when the flight was in progress, the sky was still overcast. The flight was in full swing when first encountered at about 5:00 p.m., and it persisted, with little or no decline, until nightfall, at about 7:30 p.m.

Three swarms developed in the homesite area. Each hovered over a conspicuously bare spot in the weed-grown yard, in particular a garbage pit, the corner of a collapsed stone wall, and a pile of rotting wood. Only the swarm above the garbage pit persisted throughout the observation period; the other two did not form until about 7:00 p.m. The swarms were roughly circular in shape and highly variable in size, containing at various times from approximately fifty individuals to none at all, and ranging in diameter up to about six feet. Their centers were usually located from five to six feet from the ground but occasionally shifted temporarily under the force of the wind to as low as a few inches from the ground surface or as high as ten feet from the ground. The attraction of the swarms to the bare spots mentioned was absolute. Occasional gusts of wind shifted the ants away or dispersed them altogether, but they quickly re-gathered in a swarm over the original spot.

Males made up the bulk of the swarms. These hovered more or less stationary and facing in an upwind direction when the wind was blowing, but flew zig-zag back and forth within the limits of the swarm when the air was relatively quiet. New individuals were constantly approaching from various directions out of the nearby juniper woods, while older members of the swarm were simultaneously being blown away downwind or dropping out as they successfully mated with queens, so that the membership of the swarm was always turning over. The origin of the males was not determined, but very likely they were emerging from nests in the near vicinity. Two nests of

sitarches, containing mature males, were found in the juniper woods within forty feet of the swarms. The males of the garbage-pit swarm seemed to appear in four principal "waves" during the observation period.

Females flew in slow, even circles through the swarms of males. No more than five were seen in a single swarm at a given time. Each persisted only several minutes or less (in one case, five minutes) before being mounted by a male and dropping from the swarm. The complete act of mating was observed on six occasions. In each case the male seized the female from above, whereupon both ceased flying and spiralled to the ground together. Upon reaching the ground, and not before, the male inserted its genitalia, taking from several seconds to nearly a minute to complete the act. After attachment, the male remained perfectly immobile, while the female either remained immobile or (on two occasions) proceeded to walk slowly over the ground. The male remained attached for one to two minutes and was finally dislodged by the female, who doubled up and pushed the male away with her head or (in one case) pinched the male's abdomen gently until it released its hold.

On two other occasions the pair broke apart while falling from the swarm, thus thwarting copulation. In both cases the separated individuals immediately took flight again upon reaching the ground, or at least attempted to do so. It is interesting to note at this point that occasionally females would light on the observer's shirt when he stood too near the swarm. The males in the swarm made no attempt to approach them under these conditions, and it was clearly necessary for them to re-enter the swarm in order to be successfully mated.

Following successful copulation, the males did not attempt to fly again but walked about on the ground, soon to fall prey to the legions of *Conomyrma pyramica* workers that were foraging everywhere in the vicinity. Some of the females may have also succumbed to the attacks of the *Conomyrma* workers, but this was never observed. Immediately after copulation those that were followed by the observer proceeded to walk along at a steady but un-

hurried pace until they encountered a pebble or blade of grass under which they could conceal themselves. Dealation thereafter followed, the female drawing her hind legs, one at a time, forward against the wings until the latter broke off. After dealation, the females continued to run over the ground, evidently in search of a permanent nest site. One dealate queen was found lodged in a cavity under a small rock within the homesite area.

Discussion. Several principal conclusions can be drawn from the above observations:

(1) It is almost certain that the individuals comprising the swarms were drawn from multiple nests. Incoming males were seen to approach from many directions. Moreover, it does not seem possible that all of the males in the individual swarms, which were changing in membership constantly, could have been supplied by a single nest. *Pheidole sitarches* apparently does not form very large colonies; those near the nuptial flight area appeared to contain no more than two or three hundred workers and could not have supported many more males at maximum capacity. It is likely that the swarms were formed originally by individuals attracted to the open spots in the homesite area, and thereafter the swarms, oriented to these spots, served as the principal attractant foci for individuals flying in from the outside. Mixed swarms, of course, result in genetic outcrossing and increased population variability, processes that are generally of positive adaptive value.

(2) The *sitarches* flight is of such a highly specific and transitory nature as to seemingly insure that other *Pheidole* species occurring in the same area are excluded. Nearly all of the females reaching the swarm are quickly fertilized. Moreover, each female is fertilized by only one male, thus limiting the potential genetic diversity of single colonies.

(3) The nuptial behavior is also of such a nature as to limit greatly the dispersal power of the species. It is probably true that in some species of ants the fertilized queens continue flying after leaving the nuptial swarm, thereby increasing their dispersal potential, especially if they fly upward and are caught in upper air currents.

But in *Pheidole sitarches* the female is fecundated on the ground directly beneath the nuptial swarm and does not attempt to fly afterward. It is clear that in a single generation this species is able to increase its range only by that distance over which the males form swarms away from their home nests. This limiting phenomenon may be more common in the Formicidae than previously realized. It will be recalled that ants generally have effected little dispersal to isolated oceanic islands. Polynesia, for instance, contains an extremely sparse endemic fauna, while the sharp diminution of the endemic Melanesian fauna from New Guinea eastward suggests that ants in this part of the world have relatively limited dispersal powers. Another line of evidence is that some ant species in Melanesia with flightless, ergatoid queens (e.g., *Leptogenys diminuta, L. foreli*) have dispersed farther through the outer archipelagoes than most stocks with normal winged queens. Furthermore, some of the most widely distributed groups with winged queens (e.g., *Colobopsis, Turneria*) are arboricolous and could conceivably have been carried about as entire colonies in storm-blown twigs and branches. Further study may show that ants are generally limited in dispersal powers because of peculiarities in the organization of the nuptial flight similar to those described here for *Pheidole sitarches*.