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Objectives

This research is part of a continuing, broad-scale field study of both male and female behavior in solitary, ground-nesting wasps. Emphasis at the present time is on the genus Philanthus (Hymenoptera, Sphecidae). Earlier work in Jackson Hole (Evans, 1970, 1973) had revealed the presence of large nesting aggregations of three species of this genus. Since that time we have come to appreciate that male mating strategies are deserving of detailed, comparative study; we are also aware of details of nest structure that need to be clarified. The ultimate goal of these studies is the preparation of a monograph on the comparative behavior of the species of Philanthus. More particularly, the objectives of our study in Jackson Hole in July, 1977, were as follows.

1. Study of male mating strategies in Philanthus zebratus, at a nesting aggregation of this species about 15 km SW of the Moran Post Office.

2. Similar studies of P. pulcher and P. crabroniformis at known sites about 4 km W of the Moran Post Office, near the former site of the Research Station.

3. Gathering of further data on nest structure in all 3 species.

Procedures

The first two weeks of July represent the height of the nesting and reproductive season of P. zebratus and we therefore spent every clear day at the aggregation of that species, with either 2 or 3 observers. Nests of females and sleeping burrows of males were located, marked, and mapped. Individual males were marked with Testor's paint in order to follow their movements. Several nest excavations were made in late July.

The last two weeks in July were devoted mainly to similar studies on P. crabroniformis, which emerges somewhat later than zebratus. Unfortunately, P. pulcher overlaps both species and we were unable to devote much time to this species, but we did make preliminary studies. We also missed the very beginning of the active season for both pulcher and zebratus because of the very early summer in Jackson Hole. We hope to try to rectify this next summer.

Males of all three species were collected in Bouin's fixative for study of development of the mandibular glands.

Results

Although males of P. zebratus are very aggressively territorial in at least two sites in Colorado, the Jackson Hole population exhibited very different behavior which appears to be unique among solitary wasps. About 100 females and 100 males were present during the summer of 1977. Females nested over an area measuring 15 x 60 m. They provisioned their nests with paralyzed bees and wasps. Orientation flights took the females 3-5 m high over their nests, and they returned with prey at about this same height.

Males spend the night in shallow burrows in the soil, as is usual in this genus. In the morning they emerged between 1030 and 1100 hrs and, often after visiting flowers for nectar, stationed themselves on the ground or low herbs in the nesting area. The spacing of perched males was very variable, but sometimes they were stationed less than 5 cm apart. Perched males did not harass other perched males or females that were digging. Occasionally they flew toward a passing male, but they showed no site attachment whatever and moved about freely.

Between 1113 and 1117 on four different days (despite small differences in air temperature) males began to rise in the air periodically. From then until mid or late afternoon there was a canopy of flying males at 3-5 m above the nesting site (the same height to which the females fly during orientation and at which prey-laden females return). A male's flight began with a quick ascent which was often vertical but sometimes deviated from the vertical by as much as 30 degrees. When males reached a height of 3-5 m they suddenly assumed horizontal flight paths, moving slowly or drifting with the wind for several meters. During this flight they would rise of fall a short distance and turn frequently. Upon completion of a flight, males would drop quickly to the ground. When dropping from a stationary hover the descent was nearly vertical, but when dropping during forward flight the angle was as much as 45 degrees.

Duration of the flights we measured varied from 4 to 17 seconds ($\bar{x}$ = 13, N = 20). The duration of stops on the ground between successive flights varied from 5 to 35 seconds ($\bar{x}$ = 19, N = 20). Time spent on the ground varied as a result of several factors. If a male was undisturbed by passing insects (including conspecifics) he remained longer. When two males were perched within a few cm of one another, if one ascended the other usually followed, shortening his total perch time on the ground.

Each day the number of ascending flights counted in one portion of the mating area was greatest near midday and tapered off slowly in the afternoon (Fig. 1). When in flight, males approached or chased any fast-moving object that passed near them, most commonly conspecific males but sometimes other insects and on one occasion a hummingbird. They readily changed their flight paths to pursue for a short distance stones thrown in the air at a suitable height. Individual males moved about within the swarm, and commonly did not return to the place on the ground from which they started. In 18 of 20 cases, males landed at least a meter from their initial position, and usually much more. Thus it seemed evident this behavior was not merely an extension of territoriality on the ground.

Many interactions were noted between males in the swarm. Males approaching one another would often swirl about one another in tight circles. In other cases one would pursue the other a short distance, occasionally to the ground if he descended. In no case did we observe obvious butting or grappling, as occurs

among territorial males of this and other species at other localities.

Since the peak of male flying activity occurred each day at the time of most female orientation flights and their initial returning flights with prey, and at the appropriate height, we assume that the flights served to intercept females when they were most likely to be receptive. On four occasions males were seen to pursue conspecific females, two of which had prey. These four interactions were more prolonged and intense, the male following the female to the ground after initial contact and in some cases actually striking the female, presumably in an attempt to grasp her. In a fifth instance, a pair was seen in copulo about 5 m above the nesting area. Immediately after they were spotted, they quickly dropped to the ground and remained coupled for several minutes. We observed 3 other copulations, all on or near the ground, all lasting several minutes (up to 5). Although they sometimes changed their perches while coupled, they did not rise more than a meter above the ground. In addition, as mentioned above, we observed no initiation of contact between males and females at ground level. Thus we assume that pairing occurs at the level of the swarm.

Males of P. crabroniformis also spent the night in shallow burrows within the nesting area of the females. However, in the morning (0930-1030) they merely perched for a few minutes and then flew off to nearby flowers, chiefly Solidago. Here they took nectar intermittently throughout the day and from time to time pounced upon females visiting these flowers either for nectar or to catch bees. Marked males showed no inclination to remain constant to a particular group of flowers.

In contrast, males of P. pulcher were distinctly territorial, exhibiting what Alcock (1975) has called "serial territoriality." That is, certain plots of bare ground were continually occupied during sunny hours, but not always by the same male. We have attempted to quantify the nature and timing of interactions with adjacent males. Males of this species, like several others, mark stems surrounding the territory with a pheromone.

Nests of the females of these 3 species are very different, and we obtained additional data on cell depth and arrangement, as well as further prey records, for these species. We also, as a bit of serendipity, obtained nesting data on two other species of solitary wasps, Pseudepipona herrickii and Crabro virgatus.

Discussion

It is apparent that there are at least 3 quite different mating strategies in the genus Philanthus, typified by the 3 species discussed above. Most species exhibit male territoriality, including other populations of P. zebratus. The adaptive value of the high, swarming flights of the Jackson Hole population of this species remains obscure. It may be related to nest density since when nests are very close together the cost of maintaining a territory among them may be too great. Another possibility is that this population, which so far as known is isolated by many km from other nesting aggregations, has evolved a novel mating strategy. It would seem adaptive to intercept females high above their nests, but this does not explain why this same strategy has not evolved elsewhere.

We feel that male territoriality is the basic male strategy in Philanthus, since most species have enlarged mandibular glands and clypeal brushes, which are associated with applying a pheromone to the periphery of the territory. This behavior has evidently been lost secondarily in crabroniformis and some other species, also in the Jackson Hole zebratus. We are still a long way from understanding the adaptive significance of these diverse strategies.

Conclusions

Species of Philanthus have evolved diverse male mating strategies, just as they have evolved differences in female nest structure and other aspects of behavior. The ecological factors with which these behavioral differences are correlated remain to be clearly demonstrated.

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Literature Cited

Alcock, J. 1975. Territorial behaviour by males of Philanthus multimaculatus (Hymenoptera:Specidae) with a review of territoriality in male sphecids. Anim. Behav. 23:889-895.

Evans, H.E. 1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. Harvard 140:451-511.

Evans, H. E. 1973. Further studies on the wasps of Jackson Hole, Wyoming (Hymenoptera, Aculeata). Great Basin Nat. 33:147-155.

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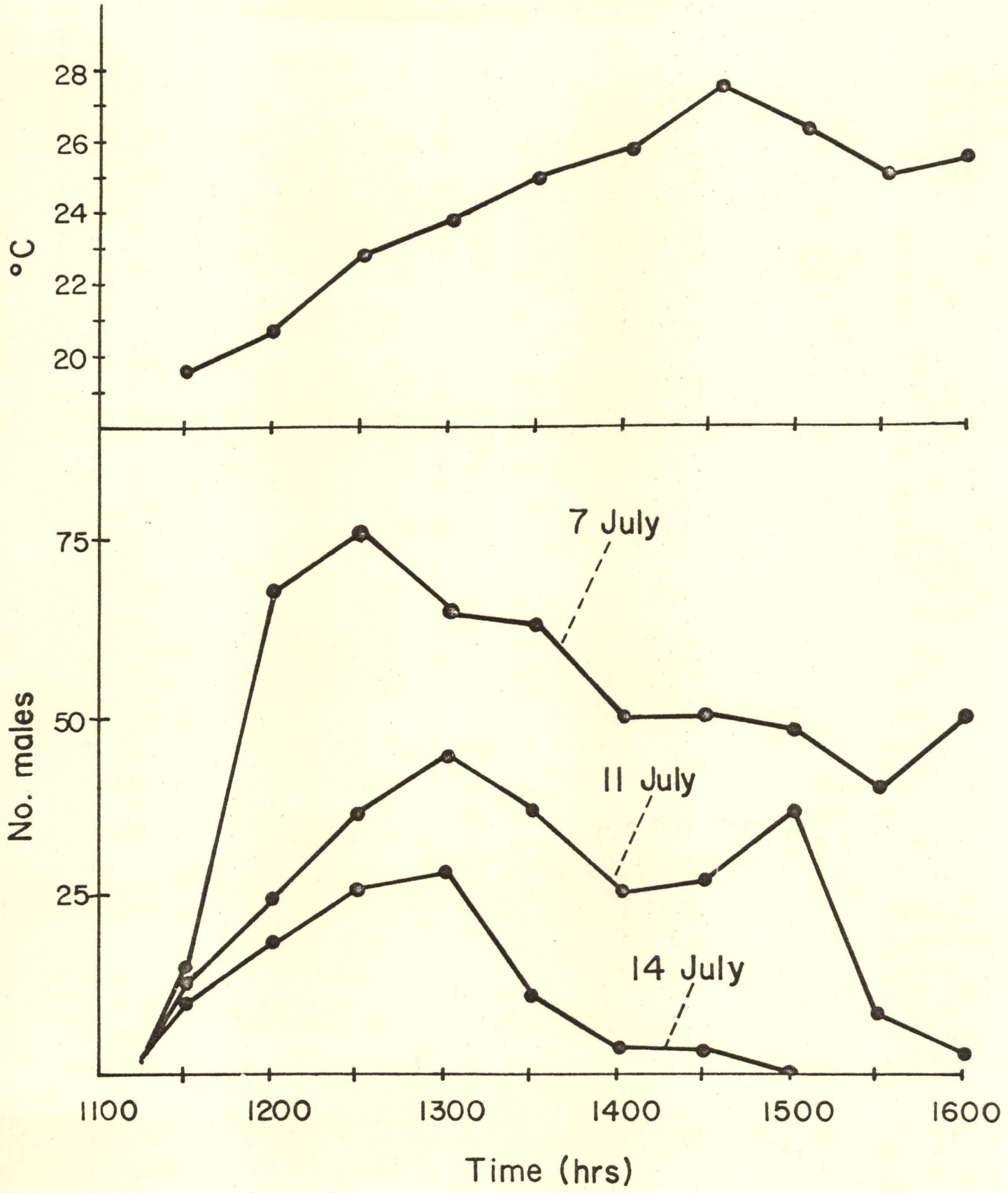

Fig. 1. Number of male P. zebratus rising into the swarm in an area about 30 m^2 near center of aggregation during a 5 minute period at half hour intervals. Temperature for one of these days (July 11) is plotted above.