

A COMPARATIVE STUDY OF MATING STRATEGIES
IN TWO SPECIES OF PHILANTHUS
(HYMENOPTERA: SPHECIDAE)

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Objectives

In the majority of animals, most or all of both pre- and post-zygotic parental investment is contributed by the female of the species. Thus, the females and their ability to invest in offspring represent a limited resource, which must be procured by a male if he is to reproduce successfully. It is on this basis that sexual selection theory predicts that there will be intense competition among males for access to sexually receptive females.

This female-biased discrepancy in the degree of parental investment is highly evident in digger wasps of the family Apecidae. The female wasps construct a nest in soil, stock it with varying numbers of insect prey on which the offspring feed and perform various behaviors aimed at reducing parasitism of the brood. Males do not participate in these activities. Therefore, we should expect that male sphecid wasps will compete among themselves in some manner for access to females. The form of the mating strategy of males should be correlated with such things as the spatial and temporal distribution of receptive females, the number of times that individual females mate and the degree and form of male-male competition.

In 1975, my graduate students and I began a rather intensive study of male behavior, in the sphecid genus Philanthus, in an attempt to describe and quantify behavioral variation within and among species and to determine the biological and ecological correlates of this variation. This is relevant both to the comprehensive behavioral study of Philanthine wasps which we have undertaken and to recent interest in theory concerning the evolution of mating strategies (e.g., Emlen and Oring, 1977; Alcock et al., 1979)

The present report describes the progress we made in 1979 in the study of two species in Jackson Hole, Philanthus pulcher and Philanthus zebratus. Research done in 1977 and 1978 is not included here.

Methodology

Most of the work to date has consisted of focal animal samples of males marked individually or by size class. Males and females were measured to the nearest 0.01 mm and marked with one or two spots of colored paint on the thorax. In addition, ad lib samples of matings, male-male fights on territories and predations were made when possible.

Results

Philanthus pulcher. We have studied the two nesting aggregations of this species which occur along the Snake River near the bridge at Oxbow Bend in Grand Teton National Park. The nesting behavior of females in the population was previously reported (Evans, 1966). The aggregations are about 400 m apart. Males defend small territories (about 0.5 m in diameter) at numerous points all along the stretch of river bank between the nesting areas and for short distance on either side of each.

Unlike P. psyche (O'Neill, in press) and P. bicinctus (Gwynne, 1978) in which males are territorial within the nesting area and set up territories at about 1000, males of P. pulcher do not begin activity until about 1200. Since females do not leave the nesting area on foraging trips until this time, it appears that males are synchronizing their activity with that of foraging females. It is possible that the males are setting up territories in the females' foraging area. This will be investigated further. Observation of marked males has shown that at least some of the males do not remain associated with any one of the two aggregations of nests.

Research during the 1979 field season concentrated on the characteristics of males which determine success in male-male aggressive interactions. Preliminary evidence from 1978 suggested that larger males won contests. Therefore we marked, measured (head width), and released 263 males so that we could observe interactions between males of known size. Males in the population had a mean head width of 2.32 mm (N=263), while females averaged 2.75mm (N=98) (Figure 1).

Competition for territories is intense. At the peak of seasonal activity there were at most 50-60 territories associated with the two aggregations. These were contested for not only by the 263 males that were marked but also by many unmarked males. In 1979, individual territories were observed for 499 minutes. During this period the resident males interacted with 24 intruding conspecific males (mean-2.88 interactions per hour).

Contests between males may or may not include physical contact. Non-contact interactions consist of two males rapidly swirling about one another, 10-15 cm above the territory. Ten percent of observed interactions of this type resulted in the intruder usurping possession of

the territory (N=20). Contact interactions included butting, grappling and probably biting. Twenty-six percent of these interactions ended with the intruder usurping the territory (N=31).

Size (or something associated with it) was indeed the characteristic of males that determined success in contests (Table 1). Only two of the forty-seven contests in which the males were of different size resulted in the smaller male winning. In these two cases, the winner was in the next smaller size class. Thus, there is a strong correlation (rank correlation coefficient=0.90) between male size and percent contests won (Figure 2; this includes interactions in which the size of only male was known; N=120).

Matings occurred when females flew upwind and landed in the territories. The female is probably attracted by a pheromone deposited on the territory by the male. Males were collected for chemical analysis of gland contents. Dr. Justin O. Schmidt of the University of Georgia is now attempting to determine the identity of the sex pheromone. If it is identified, field bioassays will be conducted next summer.

Philanthus zebratus. We originally reported that males in the Jackson Hole population of this species swarmed above the nesting area, intercepting females as they flew to and from nests (Evans and O'Neill, 1978). Since then we have found that there are also territorial males in the population. Last year eleven territories were found.

Males on territories and "high flying" males were generally of different sizes. Territorial males averaged 3.0 mm in head width (range 2.3-3.3 mm; N=23). No single male was observed to undertake both strategies. Thus, it appears that there are not only alternative mating strategies between populations of this species but also within the population at Jackson Hole.

Behavior of territorial males is apparently identical to that displayed by males of this species observed in southern Colorado (O'Neill and Evans, unpublished). There is competition for the available sites and the size of the male determines his success in aggressive contests.

Conclusions

Although this study is incomplete, several conclusions can be made at this point. In both P. pulcher and P. zebratus there is intense competition among territorial males. Larger males in the population have the advantage in aggressive interactions. In the Great Sand Dunes population of P. zebratus we have found that the mean size of males which hold territories is higher than the mean for the general population. Both species in Jackson Hole will be tested for this

next year. At this point, it also appears the males synchronize their activity period with that of females.

When the project is completed, comparison between populations and species of Philanthus should allow us to determine what aspects of female biology are relevant to the evolution of male mating strategies and to analyze the effects of male-male competition on male success. We also hope to make the first detailed analysis of the use of a sex pheromone in digger wasps.

Literature Cited

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FIGURE 1. SIZE DISTRIBUTIONS OF FEMALES (EMPTY BARS) AND MALES (SOLID BARS) OF Philanthus pulcher.

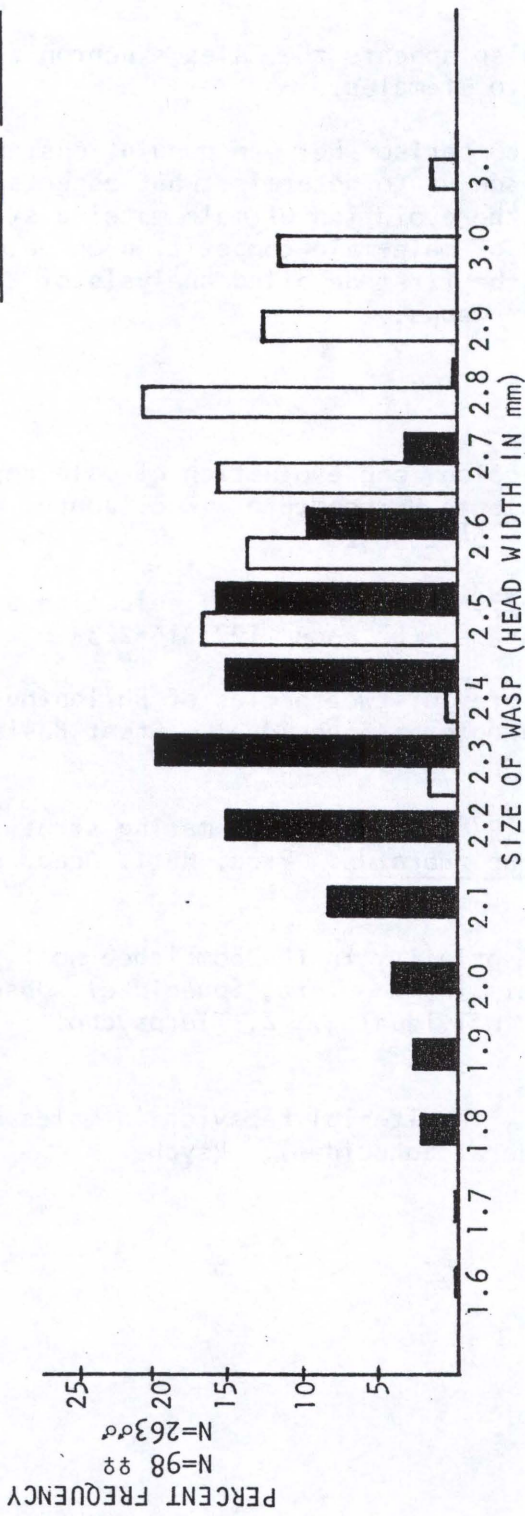


FIGURE 2. PERCENT CONTESTS WON BY MALES OF DIFFERENT SIZE CLASSES (N=120 MALES).

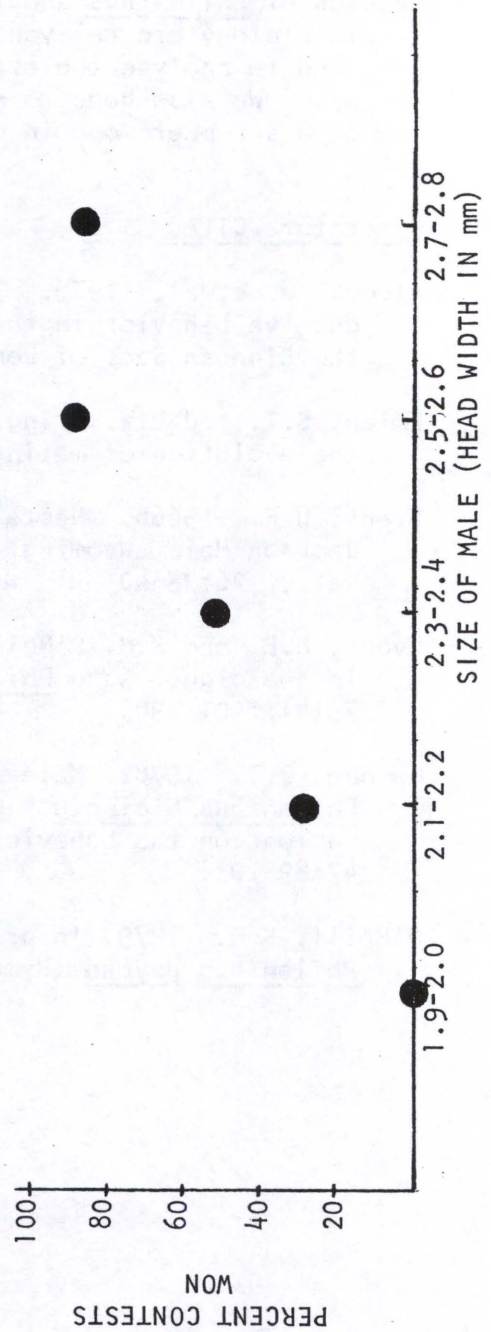


Table 1. The relative size of winners of territorial contests in Philanthus pulcher.

Result of Interaction	Relative Size of Winner		
	Larger	Same	Smaller
Resident Won	39	2	0
Intruder Won	6	2	2
Total	45	4	2
Percent of Total	88.2	7.8	4.0