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SHORT COMMUNICATION

Does *Polistes instabilis* de Saussure (Hymenoptera: Vespidae) Investment Predict Nest Defense?

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Introduction

Vertebrates have played an important role in the evolution of social wasp defensive behaviors (Schmidt, 1982; Turillazi, 1984; Starr, 1985). While many have investigated the division of labor in wasp colonies, relatively few have looked at defensive behaviors (Jeanne, 1991; Jeanne and Keeping, 1995; O'Donnell *et al.,* 1997; Smith *et al.,* 2001). Defensive behaviors of *Polistes* wasps can easily be observed and induced with a vertebrate predator mimic, due to their small colony size and simple, unenveloped nests. In *Polistes fuscatus* (Fab.), aggressiveness was positively correlated with presence in the nest of reproductive destined brood but not worker-destined brood (Judd, 1998). Judd inferred that reproductive brood were a form of direct reproductive investment and worker brood an indirect investment; thus reproductive brood should be defended more strongly.

In this study, I simulated attacks with a bird model on colonies of tropical species, *Polistes instabilis* de Saussure and compared the defensive behaviors with colony level characteristics. Specifically the proposition of Judd (Judd, 1998, 2000) was tested in that one would expect to find a strong relationship between aggressiveness and the amount of investment. This was accomplished by assessing the relationship between two behavioral responses and three colony characteristics that correspond to measures of investment: nest size, the number of pupae and the number of wasps present on the nest. *Polistes instabilis* is one of the most common species of *Polistes* in the dry forests along the western slope of tropical America from Mexico to Costa Rica (Richards, 1978).

Materials and Methods

This study was performed in Guanacaste Province, Costa Rica at the Organization for Tropical Studies field station at Palo Verde National Park (10°16′N, 85°14′W) between 28–29 July, 1999. Most of Guanacaste is characterized by a pronounced dry season that occurs from December until May (Janzen, 1983); thus this study was performed well into the wet season. Although *Polistes instabilis* has an annual phenology involving migration to high elevation aestivation sites at the end of the wet season (Hunt *et al.,* 1999), the cycle of worker and reproductive production in *Polistes instabilis* at Palo Verde is largely unknown. However, the pupae in nests during this time were likely destined to be reproductive brood, thus representing a measure of direct investment. Although female reproductive and worker *Polistes* are virtually identical in appearance and morphology, males are readily distinguishable with their yellow faces and curved antennae. Their absence during the period of this study suggests that the population in general was not in the 'reproductive phase' where gynes and males are produced; rather possibly in the 'worker phase' where the workers are tending the reproductive destined brood (Reeve, 1991).

Seventeen colonies of *Polistes instabilis* were located along the rear of buildings and nearby trails of Palo Verde Biological Station. The numbers of cells, pupae and adults present on each nest were counted. To determine aggressiveness, a three dimensional bird shaped silhouette (~20 cm in all three dimensions) was constructed out of black cardboard and suspended from pole (~5m long) with a piece of fishing line. The bird mimic was moved near a nest of *P. instabilis* so that it mimicked a bird attack. During a period of 90 seconds the 'bird' model struck the nest three times but was otherwise held suspended by the string within 10 cm of the colony. These simulated attacks occurred during the morning hours between 8–10 A.M. Two behaviors were recorded: the total numbers of wasps that exhibited a threat response (arching the gaster and vibrating the wings) as well as the total number of wasps that attacked the bird mimic, which in turn was defined as leaving the nest and physically touching the bird. Some wasps that threatened the bird also attacked it; however specific individuals (e.g., the queen) were not identified. All counts and 'attacks' on a given colony were performed within 5 minutes of each other.

Simple correlations and regressions analyses were performed using Statistica Version 5 (Statsoft, 1996). The colony characteristics were tested for correlations and multiple stepwise regression analyses were performed to find the best predictors of threatening and attacking behaviors with respect to the simulated bird attack. Variables in the stepwise regression analyses were entered at $\alpha = 0.05$ and removed at $\alpha = 0.10$.

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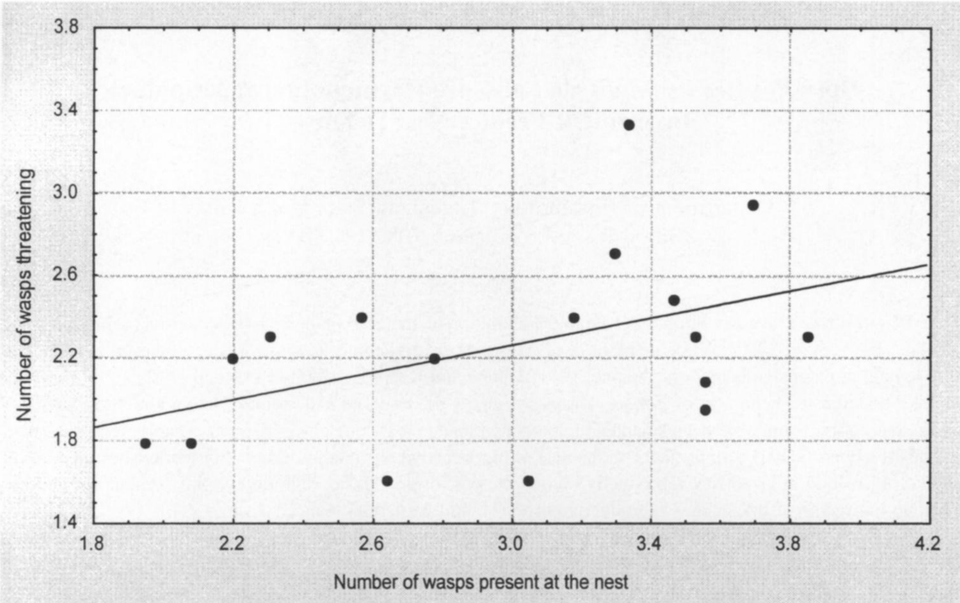

Fig. 1. Linear regression of the number of wasps threatening and number of wasps present at the nest (r^2 = 0.196, Slope B = 0.330, $F_{1,15}$ = 3.65, $P > 0.07$). Both variables are on the natural log scale.

The investment hypothesis predicts a linear relationship between the numbers of wasps defending a nest and their amount of investment. The absence of a linear relationship would indicate a constant level of defense and thus would not support the investment hypothesis. To test this hypothesis, a stepwise regression was performed with the behaviors as dependent variables and the number of cells, pupae and wasps as independent variables. The data were natural log transformed; only via this transformation did the residuals have a constant variance and fail to deviate significantly from the normal distribution.

Results

All seventeen nests had pupae and from 7 to 47 attendant wasps. Nest size ranged from 43–184 cells. All nest characteristics were positively correlated, indicating that all nests were in similar stages of development. Pearson's Product Moment Correlation coefficients for each of the correlations were as follows: No. wasps: No. pupae, $r = 0.83$, $P < 0.0001$; No. wasps: No. cells $r = 0.77$, $P < 0.0001$; and No. cells: No. pupae $r = 0.850$, $P <$ 0.0001.

The regression analyses for threatening and attacking behaviors found no linear relationships between measures of investment. The regression for threatening behavior found that the number of wasps on the nest was the most significant predictor; however the slope was statistically equivalent to zero ($r^2 = 0.196$, $P > 0.07$, Fig. 1). The stepwise regression model of the number attacking found that pupae number was the most significant predictor, however, the slope was also statistically equivalent to zero ($r^2 = 0.096$, $P < 0.225$, Fig. 2).

Discussion

The main finding in this study is the absence of a relationship between investment and defense. Defense appears to be independent of investment because a relatively similar number of wasps defended across different colony sizes. If 'decisions' to attack are based on investment, then there should have been positive relationships between defense and colony size. On the other hand, the results imply that colonies allocate a relatively fixed number of wasps to defend against an attack of a given magnitude. This suggests that natural selection has acted upon the colony to yield individual workers that will attack more readily than other workers. In other words, *P. instabilis* may allocate defensive tasks as they do other tasks such as foraging (O'Donnell, 1998). Until experiments are performed on *P. instabilis*, it will not be possible to fully determine whether wasps attack because it is in their interest (investment) or simply because they are specialized to do so. For instance, if the removal of defending wasps was followed by a similar number of defending wasps, then investment was supported. If removal resulted in fewer wasps defending, then it would appear that the removed wasps were specialized in a certain degree to perform those tasks.

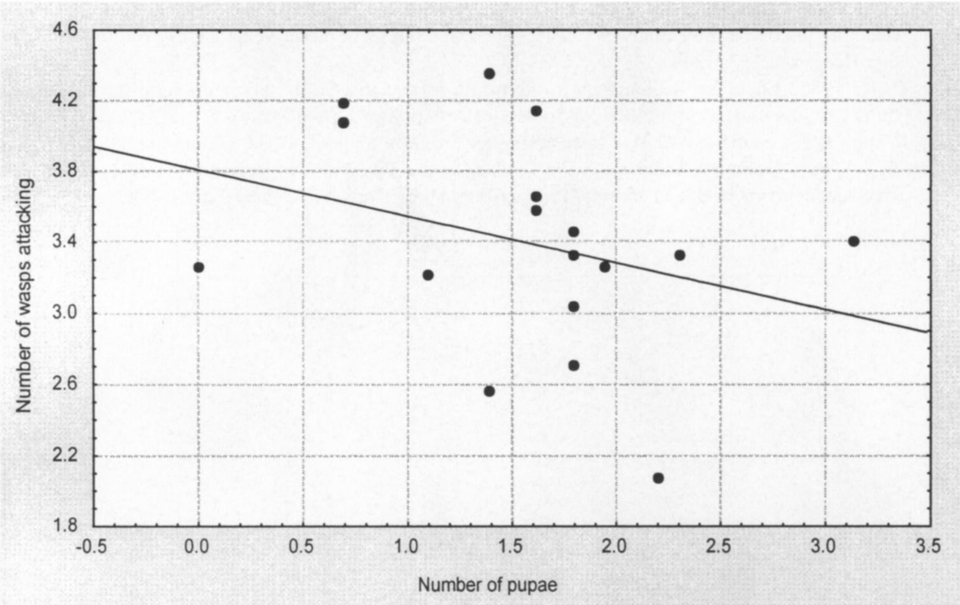

Fig. 2. Simple linear regression of the number of attacking wasps against the number of pupae ($r^2 = 0.096$, Slope B = –.366, $F_{1,15} = 1.601$, $P > 0.20$). Both variables are on the natural log scale.

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