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Condition-based alternative reproductive tactics in the wool-carder bee, *Anthidium manicatum*

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We examined alternative reproductive tactics in males of the wool-carder bee, *Anthidium manicatum*. Males either patrolled and defended well defined floral territories or wandered between them. Territory owners were larger than wanderers, large territory owners copulated more frequently than small territory owners, and males replacing removed territory owners were smaller than the original owners. These results indicate plasticity in the reproductive behavior of male *A. manicatum*, the expression and success of which is ultimately determined by body size relative to other males in the population. Although female visitation frequency was similar on sites defended by large and small territory owners, large males copulated more frequently. Thus, our data raise the possibility that females are not passive participants in mating behavior but rather are actively choosing larger males.

KEY WORDS: behavioral plasticity, reproductive tactics, resource defense polygyny, *Anthidium manicatum*.

INTRODUCTION

Anthidium manicatum, the wool-carder bee, is an ideal organism for studies of alternative reproductive tactics. *A. manicatum* have a resource defense polygynous mating system, in which some males patrol, defend, and mate on well defined floral territories, while other males wander between territories and secure copulations serendipitously (HAAS 1960, SEVERINGHAUS et al. 1981). Territory owners tend to be larger than wandering males and, among territory owners, larger males appear to have higher quality territories (SEVERINGHAUS et al. 1981) and secure more copulations (SEVERINGHAUS et al. 1981, MÜLLER 1987).

We examined the plasticity of the territory ownership tactic in *A. manicatum*. Males were captured, color-marked, measured, released and observed. During observational scans of known territories, we recorded both the number of female visitations to each site and the number of ensuing copulations. These values were

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compared between large and small territory-defending males. To test experimentally the hypothesis that relative male size is an important determinant of successful territory acquisition and defense, territory owners were removed and replacement males were allowed to establish ownership. Replacement males were then captured, measured and compared in size to the original territory owners. Thus, we examined the effect of male size on territory ownership, copulation frequency and female visitation.

MATERIALS AND METHODS

General methods. Anthidium manicatum were observed in the fall of 1994 in the New York State Herb Garden, Cornell University. Males (n = 32) were captured with sweep-nets, chilled in an ice-filled storage container, measured with calipers (maximum eye-to-eye head diameter), color marked on the thorax and abdomen with Testor's Enamel paint, and returned to the capture site.

Two categories of males were identified: territory owners and wanderers. Territory owners (n = 13) were individuals exhibiting patrolling and territory defense behaviors (as described in SEVERINGHAUS et al. 1981) and wanderers (n = 19) were individuals in which these behaviors were absent. The Herb Garden is distant from the nearest known territorial sites, and defended territories within the Herb Garden were easily located. Wanderers were thus unlikely to be immigrant territory defending males or males defending cryptic territories. Territory boundaries were determined by observations of the territory owner's flight pattern. Data were collected by seven observers.

Copulation study. Between 10:00 and 12:00 hr on 8 September 1994, territory owning males were observed for 10 min periods (n = 36) during which the number of copulations and female visitations were recorded. Any successful mount during the observation period was recorded as a copulation (as described in MÜLLER 1987). A visitation was recorded when a female entered a male's territory; visitation rates were measured from scans of the territory made every 2 min for a total of six scans in a 10 min period.

Male removal study. Between 10:00 and 12:00 hr on 13 September 1994, eight territory owners were removed, chilled, and stored in a cooler. Replacement males (n = 13) were identified using the same criteria as that for identifying original owners. Replacement males were captured, chilled, and measured. Five territories were replaced twice after successive removals. All males were released at the conclusion of the test period.

Statistical procedures. The original territory defending males were divided into two size-based groups: large and small. Large males had head diameters above the 4.5 mm median of all territory-defending male head diameters; small males had head diameters less than 4.5 mm. Head diameters are positively correlated with body size and thus are an indicator of overall size (SEVERINGHAUS et al. 1981, MÜLLER 1987). Use of parametric paired and unpaired t-tests was justified based on the roughly Gaussian distribution of the raw data. One-tailed tests were used when the alternative hypothesis was based on results from previous research. All descriptive statistics are presented as means ± standard errors.

RESULTS

Territory owners were significantly larger than wandering males (territory owners: 4.49 mm ± 0.03; wandering males: 4.34 mm ± 0.04; one-tailed t-test: $P <$

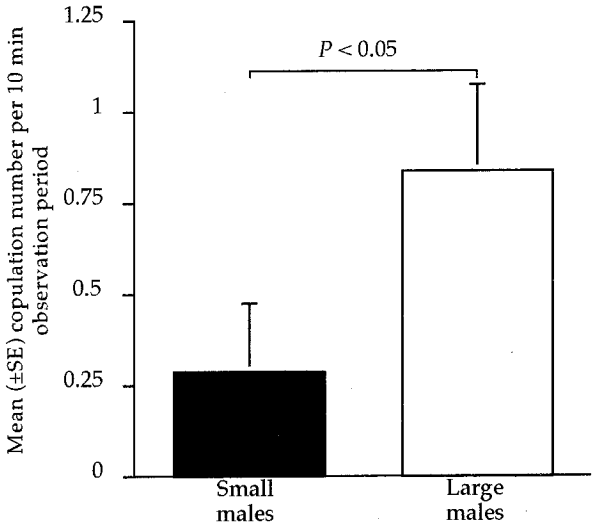

Fig. 1. — Mean number of copulations per 10 min observation period for small males (n = 7) and large males (n = 6).

0.01). Among territory owners, large males (n = 6) copulated significantly more frequently than did small males (n = 7, Fig. 1) while female visitation did not significantly differ between the two groups (large males: 0.85 ± 0.14 visitations/10 min; small males: 0.63 ± 0.13 visitations/10 min; one-tailed t-test: $P > 0.14$).

After removal of eight territory owners (mean head diameter: 4.48 mm ± 0.03), territories were re-established by significantly smaller males (first replacements: n = 8, 4.29 mm ± 0.10; paired one-tailed t-test: $P < 0.03$; all replacements: n = 13, 4.24 mm ± 0.07, one-tailed t-test: $P < 0.01$). Replacement males did not differ in size from the original wandering males (two-tailed t-test: $P > 0.20$).

DISCUSSION

The reproductive behavior of male *Anthidium manicatum* is determined by relative body size, with larger males selecting territory defense (see also SEVERINGHAUS et al. 1981, MÜLLER 1987). However, being a territory owner does not guarantee a fixed amount of reproduction, since smaller territory owners had fewer copulations than larger males (Fig. 1). The observed decrease in fitness payoff for small relative to large territory owners (Fig. 1) may be attributed to energy expenditure in defending the site against larger males (SEVERINGHAUS et al. 1981, MÜLLER 1987) and/or the inability of small males to mate on their territory (HAAS 1960; but see SEVERINGHAUS et al. 1981). Our data, however, are consistent with a third explanation: since female visitation rate did not differ between territories controlled by large or small males, females may be choosing larger males with whom to mate (see also ALCOCK et al. 1977).

Our removal experiment indicates that males display condition-dependent alternative mating tactics. Replacement males were consistently smaller than the original territory owners, which suggests that (1) large males are better at defending

territories and (2) replacement males were from the wanderer population. Condition-based alternative phenotypes are expected to have a switchpoint where the fitness payoff for either tactic is identical (reviewed in GROSS 1996; Fig. 2). At points above or below the switchpoint, individuals are expected to display the phenotype that has the highest average fitness payoff. In undisturbed *A. manicatum* populations, the switchpoint in the male reproductive decision is determined by the relative body sizes of territory owners and the wanderers (Fig. 2A). After removal of territory owners, the switchpoint appears to have been re-set such that some wanderers reap a fitness payoff for switching to the territory-owner strategy (Fig. 2B). This result suggests individual plasticity in the expression of either reproductive tactic.

In conclusion, our results indicate that (1) territory owners are larger than wanderers, (2) large territory owners copulate more frequently than small territory owners, and (3) males replacing removed territory owners are likely to be former wanderers. These results indicate plasticity in the reproductive behavior of male *A. manicatum*, the expression and success of which is ultimately determined by body size relative to other males in the immediate population.

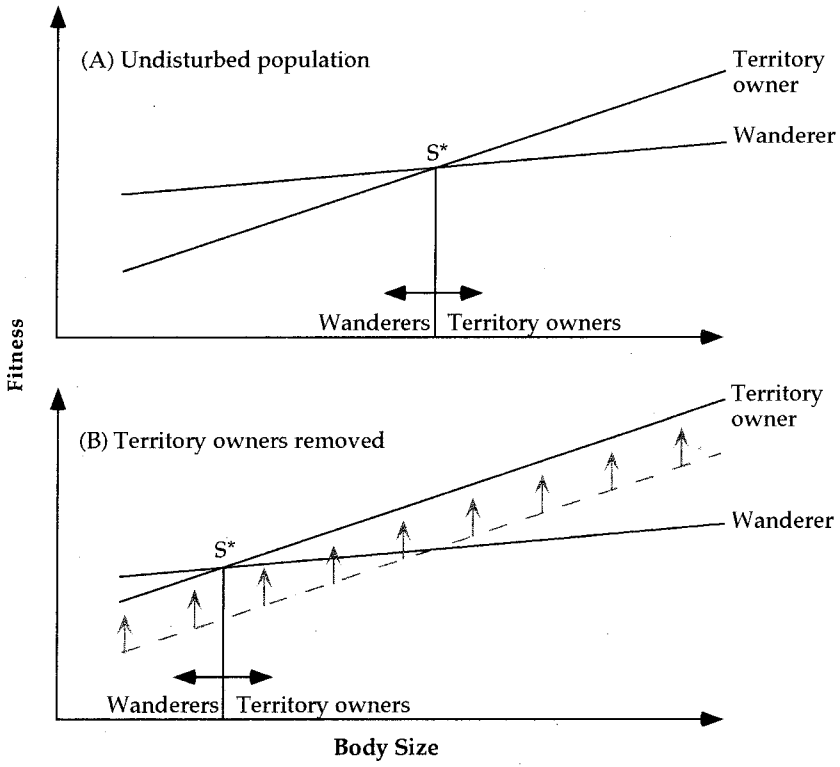

Fig. 2. — Hypothetical relationship between fitness, body size, and size thresholds for switching tactics. Each line represents the tactic-specific expected fitness payoff for a males as a function of body size. S* indicates the point where fitness payoffs for both tactics are equivalent. Above or below S*, individuals are expected to display the phenotype with the highest payoff. (A) represents the undisturbed population, (B) represents the population with territory owners removed. The territory owner line is shifted up (i.e. has a higher intercept) after removal of the original territory owners. (Adapted from GROSS 1996).

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REFERENCES

ALCOCK J., EICKWORT G.C. & EICKWORT K.R. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. *Behavioral Ecology and Sociobiology* 2: 385-396.

GROSS M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11: 92-98.

HAAS A. 1960. Vergleichende Verhaltensstudien zum Paarungsverhalten solitärer Apiden. *Zeitschrift für Tierpsychologie* 17: 402-416.

MÜLLER U.G. 1987. Dimorphic males in the European wool-carder bee *Anthidium manicatum* (Megachilidae: Hymenoptera). *Cornell University Thesis.*

SEVERINGHAUS L.L., KURTAK B.H. & EICKWORT G.C. 1981. The reproductive behavior of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the significance of size for territorial males. *Behavioral Ecology and Sociobiology* 9: 51-58.