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COOPERATIVE FORAGING FOR LARGE PREY BY *PARATEMNUS ELONGATUS* (PSEUDOSCORPIONIDA, ATEMNIDAE)

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ABSTRACT

Interrelatedness among colony members and predation competence through cooperative foraging have been proposed as factors which act to maintain an atypically high level of social organization in the pseudoscorpion, *Paratemnus elongatus*. In this paper we report on two sets of field observations consistent with these hypotheses: 1) female-bias in sex ratio, and 2) the ability of *P. elongatus* to capture unusually large, heavily-armored prey. Cooperative foraging behavior enables this pseudoscorpion to exploit ant prey (*Cephalotes atratus*) thirty times it own mass.

INTRODUCTION

Paratemnus elongatus (Banks) exhibits the highest level of social organization known among pseudoscorpions (Brach 1978). In the laboratory, immature instars communally spin and occupy silken nests used for molting, and adults and penultimate instars (tritonymphs) engage in cooperative predation (Brach 1978). These social behaviors are of particular evolutionary interest since pseudoscorpions are predominantly solitary and often intraspecifically aggressive (Weygoldt 1969; Zeh 1987). In fact, in other pseudoscorpions species, e.g., *Dinocheirus arizonensis* (Banks) and *Parachelifer hubbardi* (Banks) from Arizona, and *Cordylochernes scorpioides* (L.) and *Semeiochernes armiger* (Balzan) from Panama, we have observed numerous instances of cannibalism involving adults and nymphs preying upon same or earlier stage instars in both field and laboratory situations (personal observations).

Brach (1978) speculated that the evolution of cooperative behavior in *P. elongatus* was linked to both interrelatedness among colony members and enhanced foraging proficiency resulting from group predation. Here we provide the first quantitative data on colony composition and sex ratio in *P. elongatus* and describe field observations of cooperative foraging behavior which lend support to Brach's hypothesis.

METHODS

Between April 1988 and December 1989 we collected *P. elongatus* from beneath the bark of live or recently fallen trees, including *Miconia argentea*, *Bursera simaruba*, and *Tetrathylacium johansenii*. The pseudoscorpions generally occurred in discrete clusters (colonies) beneath sections of bark. Collections were made by brushing whole colonies into a plastic bag held firmly against the trunk of the tree. We collected them from Cerro Luisa, Gamboa, Camino de Cruces Trail, Barro Colorado Island, and Gigante Peninsula, all of which lie in tropical moist forest of the former Canal Zone, Republic of Panama. Descriptive statistics on colony composition were computed using SAS (SAS Institute, Inc. 1988). In order to test for departure from 1:1 sex ratio, we treated each colony, not individual pseudoscorpions, as a replicate. A paired t-test of the number of female minus male individuals in each colony was carried out on log-transformed data to equalize variance. In addition, 20 first instars (protonymphs) from three colonies were reared to adults in the laboratory to assess the correspondence between primary and adult sex ratio.

Voucher specimens of the pseudoscorpion have been deposited with W. M. Muchmore of the University of Rochester and with V. Mahnert of the Muséum d'Histoire naturelle, Switzerland. Both taxonomists have indicated that species identification of this pseudoscorpion is tentative. *Paratemnus elongatus*, which has been recorded from southeastern U.S.A., Central America, Dominica, and northern South America, is very similar morphologically to *P. nidificator* (Balzan) from Paraguay and P. minor (Balzan) from Brazil, and Mahnert believes that further study may show the three species to be synonymous (personal communication).

Observations and photographs of foraging behavior in *P. elongatus* were taken over a two-week period in April and May 1988. Seven colonies of pseudoscorpions had become naturally established over a 60 m section of chain-link fence immediately adjacent to second-growth forest in Gamboa, Panama. The colonies were located beneath gaps in metal sleeves connecting upright fence posts to the top horizontal bar. A common prey item of the pseudoscorpions was *Cephalotes atratus* (L.). Voucher specimens of the ant have been deposited with D. Quintero of the University of Panama.

A sample of ants and pseudoscorpions was dried at 50 °C to constant weight (Cahn 28 Automatic Electrobalance) in order to compare the relative mass of prey and predator.

RESULTS AND DISCUSSION

Colony composition.—Total number of individuals per collection varied between one and 53 with a mean (± SE) of 11.3 ± 2.3 (N = 23 collections). When categorized by life stage and adult sex, the mean numbers of individuals per collection are as follows: males = 1.43 ± 0.26; females = 3.22 ± 0.62; tritonymphs = 3.26 ± 0.90; deutonymphs = 2.70 ± 0.82; protonymphs = 0.65 ± 0.33. The most striking pattern which emerged was the strong female-bias in colony sex ratio, with a mean proportion of males (p_m) = 0.31 ± 0.11. This departure from a 1:1 sex ratio is highly significant statistically (t = 2.56, P =

0.009). Of the 20 individuals reared from protonymphs in the laboratory, there were 12 females, six males, and two deaths ($p_m = 0.33$). Taken together these data suggest that bias in the primary sex ratio and not sexual differences in mortality are the causes of the skewed adult sex ratio.

Population genetic models predict female-biased sex ratios in inbred populations since an excess of females acts to reduce local mate competition, i.e., competition for mates between related male offspring (see Hamilton 1967). Comparative data on a variety of species demonstrate a strong empirical link between inbreeding and sex ratio bias (Bulmer 1986). Thus our findings are consistent with (but do not prove) the hypothesis of interrelatedness among colony members. We are currently developing electrophoretic methods in order to more directly assess relatedness levels in this species.

Field observations of predation.—Corpses of medium- to large-sized insects (beetles, millipedes, and ants) were found with their appendages lodged within the entrances of the pseudoscorpion colonies. These included six specimens of the large, heavily-sclerotized cephalotine ant, *Cephalotes atratus* (see Corn 1980). On two occasions (1700 hours, 30 April 1988; 1730 hours, 2 May 1988), successful capture of and predation on live *C. atratus* were observed. With pedipalps extended, adult *P. elongatus* were assembled along the entrance of the colony to form a nearly continuous battery of chelae. As the ant walked across the colony entrance, several pseudoscorpions used their chelae to clamp onto the ant's forelegs (Fig. 1). The pseudoscorpions then pulled back into the colony, pinning the ant against the entrance. Tritonymphs converged on the ant within 60 s of capture and began inserting their chelicerae into articulations of the leg segments. Except for brief excursions, the pseudoscorpions remained at or within the nest entrance for at least 1 h after capture. After 3 h, tritonymphs were observed outside the entrance feeding on the abdomen of the ant. Comparative dry weight data illustrate the magnitude of the size discrepancy between prey and predator—the ants outweigh the pseudoscorpions by a factor of 30 (mean dry weight in mg: *P. elongatus* = 0.55 ± 0.03, $N = 11$; *C. atratus* = 16.08 ± 0.75, $N = 12$).

Observations of staged encounters made on three colonies suggest that cooperative effort is important in enabling *Paratemnus* to dispatch large prey. For each colony, a single live ant was deposited five times at the nest entrance (different ant used for each colony). Ants walking over the colony entrance escaped capture when only one pseudoscorpion managed to grasp a leg (5 of the 15 trials). Successful captures (4 of 15 trials) minimally involved three adult *Paratemnus* grasping the ant within 5 s of the first individual's attachment. In addition, ants which we forcefully dislodged from pseudoscorpions were still alive and mobile 10 min after capture, indicating that pseudoscorpions must restrain the ant for a relatively long period in order to kill it. In the remaining six trials, no pseudoscorpion was successful in grasping the leg of the ant.

Interesting observations of *Paratemnus* and *Cephalotes* have been recorded by M. L. Corn working in Colombia. Corn was perplexed by observations of *Paratemnus* sp. feeding on recently dead *C. atratus* since in other contexts this heavily-armored ant appeared to be impregnable to the attacks of predators. She observed *C. atratus* workers emerging relatively unscathed from columns of raiding army ants (*Labidus* sp.) (personal communication to W. B. Muchmore).

The potential significance of cooperative predation in *P. elongatus* is perhaps best illustrated by a quote from Oliveira and Sazima (1985): "Ants outnumber in

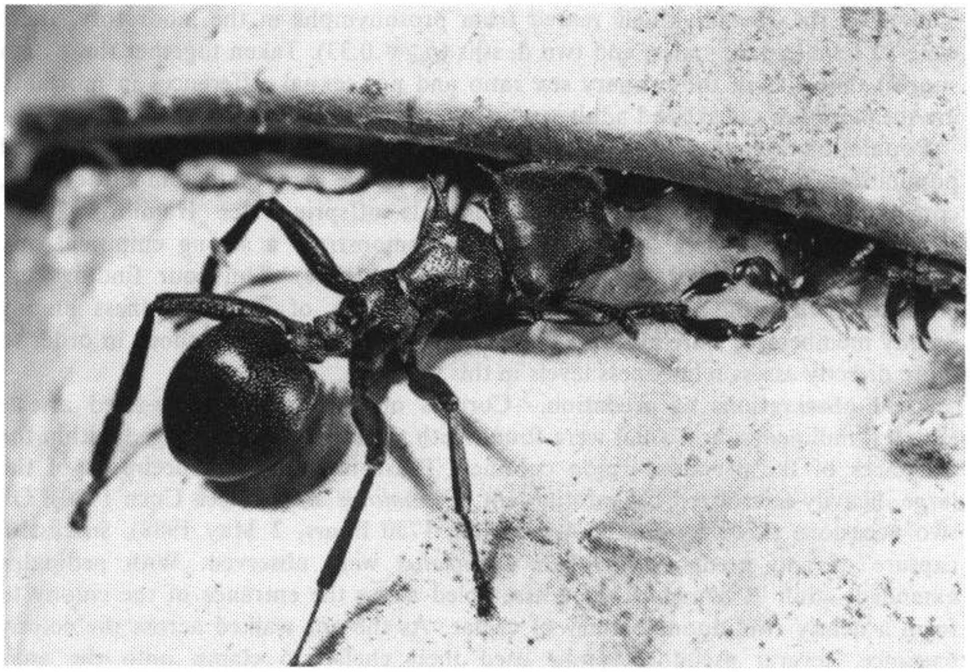

Figure 1.—Predation on a *Cephalotes atratus* worker by a colony of the pseudoscorpion *Paratemnus elongatus*.

individuals all other terrestrial animals and, although they represent a significant food resource, few predators regularly feed on them." We suggest that the ability to dispatch large prey through cooperative predation has been an important factor in the ecological success of this very abundant (Hoff 1964) and widely-distributed pseudoscorpion.

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