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Research article

Sex ratios and the distribution of elaiosomes in colonies of the ant, *Aphaenogaster rudis*

J.M. Bono* and E.R. Heithaus

Biology Department, Kenyon College, Gambier Ohio 43022, USA, e-mail: bonojm@lamar.colostate.edu, heithaus@kenyon.edu
** Current Address: Biology Department, Colorado State University, Fort Collins, Colorado 80523, USA, e-mail: bonojm@lamar.colostate.edu*

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Summary. Genetic theory predicts that workers in monogynous ant colonies with singly-mated queens should capitalize on higher relatedness with sisters than with brothers by altering the sex investment ratio of a colony in favor of females. Sex investment ratios, however, may also be influenced by the amount of resources available to colonies, in part because more mating opportunities might be obtained by investing scarce resources in males, which are much smaller than queens. Female larvae that reach a critical size by a particular point in development become queens while underfed larvae develop into workers, so workers could potentially influence the sex investment ratio of a colony by selectively feeding female larvae. In a previous experiment on the ant, *Aphaenogaster rudis*, colonies increased female sex investment after their diet was supplemented with elaiosomes, a lipid-rich food gained from a seed dispersal mutualism. In order to investigate the mechanisms producing this shift, we radio-labeled *Sanguinaria canadensis* elaiosomes with fatty acids and compared uptake among castes within a colony. The experiment was performed in both the laboratory and field. Lab colonies produced female-biased sex investment ratios, while field colonies mainly invested in males. We hypothesize that this discrepancy is related to differing levels of background food availability in the lab and field. The results of the elaiosome distribution experiment do not support a hypothesis that elaiosomes play a qualitative role in queen determination, because all individuals in a colony receive this nutrient. There is, however, support for the hypothesis that elaiosomes have a quantitative effect on larval development because larvae that accumulated more radio-label from elaiosomes tended to develop into gynes (virgin queens), while other female larvae developed into workers.

Key words: Sex ratio, elaiosomes, food distribution, queen determination, *Aphaenogaster rudis*.

Introduction

At the scale of populations, ants often produce sex investment ratios that are predicted by genetic theory (reviewed by Bourke and Franks, 1995). However, sex ratios are expressed ultimately at the colony level, and individual colonies usually heavily favor investment in either male or female reproductives (Nonacs, 1986). Thus, knowing the proximate mechanisms used by colonies to adjust sex investment is essential to understanding how sex ratio evolves in ants.

Genetic theory predicts that workers in monogynous colonies with singly mated queens should capitalize on higher relatedness with sisters than with brothers by altering the sex investment ratio of colonies in favor of females (Trivers and Hare, 1976). The fate of female larvae is not fixed genetically, meaning that individual females can develop into gynes (virgin queens) or workers. Hölldobler and Wilson (1990) identified six stimuli that influence the developmental switch between worker and queen: larval nutrition (larvae receiving more food are more likely to develop into queens), winter chilling of larvae or eggs, temperature, caste self-inhibition, egg size, and queen age.

Workers have limited control over most of these conditions but are in a position to directly influence larval nutrition. Thus, worker-controlled food distribution potentially provides a mechanism for altering the sex investment ratio of a colony. Workers could alter sex investment ratios in favor of females by selectively overfeeding certain female larvae so that they develop into gynes instead of workers. Colonies with more food could invest in females, whereas food-stressed colonies may produce relatively more male biased ratios. Thus, natural variation in food availability within a population may help to explain sex ratio variation at the colony level.

Food supplementation experiments have produced mixed results. Deslippe and Savolainen (1995) observed a shift toward gyne production in food-supplemented colonies of the ant, *Formica podzolica* and Aron et al. (2001) demonstrated