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# A test for variation in slave species work efficiency in mixed slave-maker, *Protomognathus americanus* (Hymenoptera: Formicidae), colonies

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**Abstract**

The possibility that some species of slaves might work more efficiently than others in slave-maker colonies was studied using colonies of the slave-maker ant, *Protomognathus americanus* (EMERY, 1895) that contained two slave species *Temnothorax longispinosus* (ROGER, 1863) and *T. curvispinosus* (MAYR, 1866). No difference between the contribution to foraging between the two species was found. This suggests that slaves of the less common slave species are not adjusting their behavior in the presence of another, more common slave-species.

**Key words:** *Protomognathus americanus*, *Temnothorax*, slave-maker, brood parasitism, coevolution, dulosis.

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## Introduction

The evolutionary relationship between brood parasites and their hosts has been well documented in birds (ROSKAFT & MOKSNES 1998, PAYNE & al. 2000). A host's response to an avian brood parasite can vary among populations, and different species of hosts of the same parasite vary in their ability to recognize a parasitic egg and thus differ in quality from the perspective of the parasite (BRISKIE 1992, ROSKAFT & MOKSNES 1998).

Recent work with the slave-maker, *Protomognathus americanus* (EMERY, 1895), and its host genus, *Temnothorax* MAYR, 1861, has revealed not only that some host colonies repel slave-maker attack, but that this behavior varies among populations (FOITZIK & HERBERS 2001a, b, HERBERS & FOITZIK 2002, BLATRIX & HERBERS 2003). Variation in resistance appears to be related to the slave-maker density and the density of the host relative to other locally available hosts. Further, the aggressiveness of the slave-maker towards its host also varies (FOITZIK & al. 2001a).

*Protomognathus americanus* parasitizes several hosts within the genus *Temnothorax* (ALLOWAY 1990). It has been assumed that all slaves are of equal quality. However, it would seem possible that hosts of slave-making ants may also vary in quality, just as hosts vary in avian brood parasite associations. Indeed, TRAMPUS (2001) reports that *Temnothorax longispinosus* (ROGER, 1863) workers become less efficient if the variation in worker relatedness increases. Workers in more genetically uniform nests foraged more than workers in less uniform nests. If a slave-maker population has become specialized on one host species, the less common species may respond by working less efficiently because the slave-maker cues may become more effective on the common host and less effective on the rare host. Thus, the rare host might respond similarly to the workers in genetically variable nests in the TRAMPUS (2001) study and become less efficient.

In this study, I compared the contribution to foraging of two species of slaves in lab maintained *Protomognathus americanus* colonies that contained both *T. longispinosus* and *T. curvispinosus* (MAYR, 1866). I compared the proportion of individuals of a slave species that foraged to the proportion of individuals of that species in the colony. A consistent difference in the contribution to foraging between slave species would suggest that one species is responding less to the cues produced by the slave-maker.

## Methods and materials

Collection and housing: During July 2004, eight nests containing the slave-maker *P. americanus*, and workers from both *Temnothorax curvispinosus* and *T. longispinosus* were collected on the property of the Circle H Bed and Breakfast in Bruceton Mills, West Virginia (79.78° W, 39.66° N). The site consists of 90 acres of woodlands. On this site, *T. longispinosus* is more common than *T. curvispinosus* (T.M. Judd, unpubl.). Nests were collected at a minimum of 10 m from each other to prevent collecting from the same polydomous colony multiple times (BLATRIX & HERBERS 2003). Five of the eight nests were queenright. The nests were shipped back to the Biology Department at Southeast Missouri State University.

Ants were removed from their acorn, and housed in 709 ml plastic, sealable sandwich containers with 1 cm layer of plaster on the bottom. These containers kept the moisture from escaping. A small cavity was created in the plaster with a U.S. nickel in the center of the nest box and covered by a microscope slide. A small entrance hole was carved into the plaster, allowing access to the cavity. The ants readily moved into the cavity. The ants were allowed

to acclimate to the nestboxes for two days at room temperature and were starved prior to the experiment. Although *P. americanus* colonies are potentially polydomous (BLATRIX & HERBERS 2003) and it is possible that each nest was part of a larger colony, hereafter ants collected from the same nest will be referred to as a "lab colony".

Trial: A feeder containing 0.5 M sucrose solution was placed into the arena. The feeders were made of a plastic disc (15 cm in diameter) with eight grooves carved into it. A small PVC pipe cap containing the food was inverted onto the disc allowing the ants to feed continuously. These are similar to the feeders used in many honeybee experiments (FRISCH 1967, SEELEY 1995) and used in ant experiments by JUDD (2005).

Once an ant found the feeder and started feeding on the solution, the trial was considered to have begun. From that time, the number of individuals of each species at the feeder (present on the plastic disc) was counted every five minutes for one hour. A single trial was run for each of the eight lab colonies. After the trial was completed, the total number of workers of each species in the lab colony was determined.

Data analysis: For each trial, two scores were determined. 1) The average number of foragers for each species present at the feeder for each 5 min interval during the last 50 minutes of the trial. The first 10 minutes were not used to allow the number of workers at the feeder to stabilize as nestmate recruitment occurred. 2) The maximum number of ants of each species occurring at the feeder during the trial. For each species, these scores were converted into the proportion of all foragers represented by that species. Both scores gave the same result so only the results of the mean number of foragers will be reported here.

For each lab colony, I determined the proportion of the foraging force (proportion foraged = PF) represented by *T. curvispinosus* and *T. longispinosus* and the proportion of each species of total slave species work force each *Temnothorax* species accounted for (proportion in lab colony = PC).

I used the Wilcoxon Signed-rank Test to determine if the proportion foraged was significantly different than the proportion in lab colony for both species. If the two species contribute equally to foraging, then the proportion foraged should equal the proportion in lab colony (PF = PC), otherwise the proportion foraged should be significantly higher than the proportion in lab colony for one species ($PF_1 > PC_1$; $PF_2 < PC_2$).

**Results and discussion**

In five of the eight lab colonies tested, the proportion foraged (PF) for *T. longispinosus* was higher than the percentage in the lab colony (PC; Fig. 1a, b). However, this result was not significant (T = 17, p = 0.47). In one lab colony, *T. curvispinosus* was the only species that foraged. Therefore, there was no species level difference in the contribution to foraging across all eight lab colonies.

One interesting observation from this study is that in all but one case, one species was foraging more than another (Fig. 1b). In three of the lab colonies, *T. curvispinosus* represented a higher amount of the foraging force and in four of the lab colonies, a greater proportion of the foraging force was *T. longispinosus*. This is possibly due to the fact that one species of workers may have been older than the other species of workers. Because younger workers tend to stay in the colony (HÖLLDOBLER & WILSON 1990, FRANKS & TOFTS 1994) the older species would forage more. However, the actual ages of the slaves are not known and one could argue that this result could also happen by chance if all workers have an equal probability of being recruited.

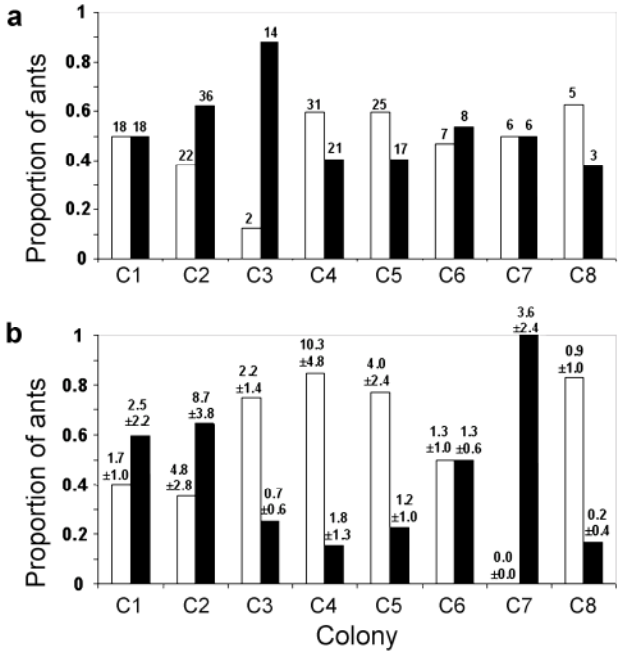


Fig. 1: The proportion of *Temnothorax longispinosus* (white bars) and *T. curvispinosus* (black bars) found a) in the nest, and b) foraging at the feeder. Each lab colony is shown separately. In graph a, actual numbers of ants are given above the bars. In graph b, the mean ± SD of the ants foraging are given above the bars.

BRANDT & FOITZIK (2004) demonstrated that some populations of *P. americanus* specialize on the most abundant host. A potential cost of host specialization is the potential reduction of the ability of the slave-makers to subdue other host species. Slave-makers that specialize on a single species might be selected to adjust their chemical cues causing workers of the more common species to work more efficiently (ALLOWAY 1982). If this change in chemical cues occurs, then other potential host species might find it harder to recognize the slave-makers as colonymates and reduce their work rate. Although this would have no effect on the slave's fitness (GLADSTONE 1981), it could reduce the fitness of the slave-maker colony. The results of this study suggest that in skewed populations the less common slave species do not reduce their contribution to foraging. Therefore there appears to be little effect of relative host species abundance on slave behavior in the population tested in this study. However, more, larger scaled experiments need to be performed to see if this pattern holds up in other populations, in other worker tasks, and how slave work efficiency compares to workers of free-living colonies.

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## Zusammenfassung

Die Frage, ob manche Sklavenarten in Kolonien von Sklavenhalterameisen effizienter arbeiten als andere, wurde hier anhand von Kolonien des Sklavenhalters *Protomognathus americanus* (EMERY, 1895) mit versklavten *Temnothorax longispinosus* (ROGER, 1863) und *T. curvispinosus* (MAYR, 1866) untersucht. Es wurde kein Unterschied im Fouragierbeitrag zwischen den beiden Arten gefunden. Das legt nahe, dass Sklaven der weniger zahlreichen Art ihr Verhalten in Anwesenheit einer anderen, zahlreicheren Sklavenart nicht anpassen.

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