

PUPA ACCEPTANCE BY SLAVES OF THE
SOCIAL-PARASITIC ANT *POLYERGUS**
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Slave-making ants of the formicine genus *Polyergus* are obligatory parasites of the genus *Formica*. To maintain a supply of slaves, *Polyergus* workers raid *Formica* colonies and capture brood, primarily pupae. Some of this brood survives to eclosion in raiders' nest, and these new workers perform their species-typical behaviors in the service of the slave-makers. Colonies of the eastern species *P. lucidus*, and of the western species, *P. breviceps*, contains only one species of slave, unlike related facultative slave-makers of the genus *Formica*. *P. lucidus* enslaves the subgenus *Neoformica*, while *P. breviceps* uses the *Formica fusca* species group (Creighton, 1950).

Formica slaves within a *Polyergus* nest rear through eclosion both the *Polyergus* brood and the brood retrieved from various *Formica* nests. An encounter between two *Formica* workers from different nests, either free-living or enslaved, is fiercely aggressive. Under laboratory conditions where mutual avoidance is impossible, injury or death usually result (Goodloe & Topoff, unpublished data). *Formica* workers may be able to perceive colony specific differences in pupae (Wilson, 1971). If slaves were inclined to ignore or destroy pupae from alien conspecific colonies, survival of captured brood would be threatened. For the myrmicine slave-maker *Harpagoxenus americanus*, Alloway (1982) has shown that the presence of the slave-makers enhances the pupae-acceptance behavior of the slaves (fewer pupae are eaten and therefore more are saved to eclose).

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This paper presents the results of three experiments designed to elucidate the relationship between enslavement and pupae acceptance in *Polygerus* and their *Formica* hosts. Experiment 1 explored the parameters of intraspecific pupae-acceptance of slave species in their free-living state. Experiment 2 considered whether association with the slave makers causes a change in the pupae-acceptance behavior of the slave species. Field studies by Talbot (1967), Cool-Kwait & Topoff (1984), and Topoff, LaMon, Goodloe, & Goldstein (1984), showed that much of the brood retrieved by the raiders is consumed. Since raiders obtain all food from their slaves, it is the slaves who are consuming the captured pupae.

The Long Island habitat of *P. lucidus* is unique in that it contains at least three slave species of *Formica*. In the nests of neighboring facultative raiders, it is common to find more than one slave species, while *P. lucidus* is found with only one. Previous research (Goodloe, Sanwald, & Topoff, 1987) has shown that a *P. lucidus* colony will almost exclusively raid colonies of the same slave species present in their nest. Another factor that might foster the host-specificity of *P. lucidus* would be differential consumption of captured pupae. If a species other than the slave species currently in residence is raided, brood from this raid might be more likely to be consumed. Experiment 3 examined whether pupae from different host species would be differentially consumed in *P. lucidus* colonies.

EXPERIMENT 1: INTRASPECIFIC PUPAE EXCHANGE (FREE-LIVING *FORMICA*)

Methods and materials

Seven free-living colonies of *F. schaufussi* (a slave species of *P. lucidus*) were collected near Rocky Point in Suffolk County, N.Y., during the summers of 1983 and 1984, and were maintained in the laboratory. The colonies were kept in 21.6 × 29.2 cm plastic boxes, with approximately 1 cm of fresh sand covering the bottom. The sides of the boxes were coated with polytetrafluorethylene to prevent the ants from escaping. Within each box, a 150 mm plastic petri dish, containing a white hydroset substrate of approximately 5 mm in depth to retain moisture, served as a nest. Honey, water, and *Tenebrio* larvae were provided ad libitum.

Table 1. Pupa acceptance by slave species workers (*F. schaufussi*)

Colony	Surviving Pupae		
	# Workers	Same	Different
F23	250	25	24
F28	550	25	23
F16	200	22	25
F24	214	24	21
F36	354	25	25
F57	208	25	24
F55	300	25	22

Correlated groups $t = 1.25$; $df = 6$; NOT SIGNIFICANT

Prior to the experiment, the queen and most of the workers from each of the seven colonies were removed from the nest and placed in a fresh box and nest dish, with food and water. The experimental colonies ranged in size from 200 to 550 workers (Table 1). After 24 hr, the queen and workers in each of the seven new nests were presented with 25 pupae, either from their own colony ("same"), or from one of the other experimental colonies ("different"). Four colonies received the "different" condition first, while the remaining three began with the "same" condition. After five days, the surviving pupae and callows were removed and counted. After another 24 hr (to recover from these manipulations), each colony was presented with 25 pupae from the alternative condition to their first presentation, and a count was made five days later.

During the summer of 1986, eleven partial colonies of *F. gnava* (a slave species of *P. breviceps*) were collected in Cave Creek Canyon, Cochise County, Arizona. Eight of these contained no queen, one contained a single queen, and the rest contained multiple queens. Laboratory colony size ranged from 81 to 500 workers (Table 2). Colonies were kept under conditions nearly identical to those described above with the exception that 16×150 mm test tubes containing about 3 cm of water and plugged with cotton were substituted for the plastic petri nest dishes, and the plastic boxes in which they were contained were 20×15 cm. Two-to-four weeks after the colonies were collected, they were subjected to the experimental procedure described above.

Results

As shown in Tables 1 and 2, no significant difference was found between the mean number of pupae accepted from the "same" and

Table 2. Pupa acceptance by slave species workers (*F. gnava*)

Colony	Surviving Pupae		
	# Workers	Same	Different
FG2	81	24	25
FG3	85	24	23
FG4	276	23	23
FG5	323	24	22
FG6	500	25	25
FG7	238	24	22
FG8	400	23	23
FG9	174	21	24
FG10	250	23	24
FG11	115	23	24
FG12	112	25	24

Correlated groups $t = 0.19$; $df = 10$; NOT SIGNIFICANT

“different” conditions for both species of *Formica* (t -test for correlated groups, *F. schaufussi*: $t = 1.25$, $df = 6$; *F. gnava*: $t = 0.19$, $df = 10$). Free-living *Formica* workers of these species treat alien conspecific pupae as their own. With the exception of *F. gnava* colony FG10, in which two pupae of the “same” condition were found in their “garbage” pile, pupae were not discarded intact from any nest and none became moldy. The number of pupae that disappeared was fairly constant in all groups despite differences in colony size. Possibly the lost pupae were defective or diseased, which might be expected to occur with a similar frequency in all groups.

EXPERIMENT 2: INTRASPECIFIC PUPAE EXCHANGE (FREE-LIVING VS. ENSLAVED *FORMICA*)

Methods and materials

Three laboratory colonies of *P. lucidus* with *F. schaufussi* slaves and six free-living laboratory colonies of *F. schaufussi* were used in this experiment, which was conducted in January and February of 1985. Each colony was handled as in the previous experiment, with queen and workers being placed in a new nest. P5, a large *P. lucidus* colony, was divided into two parts: P5(1), with a ratio of slaves to raiders of approximately 10:1, and a total of 459 ants; and P5(2), with a ratio of 1:1 and a total of 200 ants. After a 5-day period of isolation, 25 *F. schaufussi* pupae from different colonies were added to each. Five days later, the surviving pupae and callows were counted.

Results

Table 3 shows that the number of pupae surviving in the mixed nests was significantly less than the numbers surviving in the free-living *F. schaufussi* colonies ($t = 7.40$, $df = 8$, $p < .0005$). Since all colonies were on the same diet as those used in Experiment 1, and were satiated at the time of the experiment, these results suggest that captured pupae have a particular importance as a food source in the mixed colonies. Unlike the myrmicine raiders studied by Alloway (1982), the presence of these slave-makers appears to induce consumption of the alien pupae by the slaves.

EXPERIMENT 3: INTERSPECIFIC PUPAE EXCHANGE

Methods and materials

A large colony of *P. lucidus*, with *F. schaufussi* slaves, was collected during the summer of 1984 and subjected to two cooling induced cycles of reproduction. In March of 1985 the colony was divided into five smaller, queenless colonies: P5A contained 100 slaves and 26 raiders; P5B, 100 slaves and 12 raiders; P5C, 100 slaves and 25 raiders; P5D, 100 slaves and 50 raiders; and P5E, 100 slaves and 100 raiders. In addition, a colony (S) consisting of 200 workers from a free-living *F. schaufussi* colony was used for comparison.

Table 3. Pupae acceptance: free vs. parasitized slave species colony

Free Living			Enslaved		
Colony	# Workers	#Surviving Pupae	Colony	# Workers	#Surviving Pupae
F18	94	21	P3	150F* 120P**	5
F56D	82	23	P4	140F 40P	15
F76	110	24	P5(1)	415F 44P	9
F15	643	22	P5(2)	100F 100P	8
F32	781	23			
F70	100	21			
Mean		22.333			9.25

* F = *F. schaufussi* workers

** P = *P. lucidus* workers

$t = 7.40$; $df = 8$; $p < .0005$

As in the previous experiments, each group was placed in a fresh box with fresh nest dish. After 24 hours to recover from the move, all the experimental colonies, except P5A, were presented with 20 pupae from *F. nitidiventris* nests. P5A was presented with 20 pupae from *F. schaufussi* nests to check for a possible order effect. After five days, a count of surviving pupae was made in each group and all pupae were removed. Following a three-day recovery period, 20 pupae of the alternative slave species were presented to each colony. After five days another count was made and again three days were allowed for recovery. This cycle was repeated two more times, using 15 rather than 20 pupae (due to a decreasing laboratory supply), so that each colony received six presentations, three of pupae from each species for a total of 55 pupae from each.

Results

All experimental colonies consumed significantly more *F. nitidiventris* pupae than *F. schaufussi* pupae, including the group containing no *P. lucidus* workers (Table 4), suggesting that this is characteristic of *F. schaufussi* workers, whether free-living or enslaved. No correlation was found between the size of the colonies or the ratio of slaves to raiders and the amount of pupae consumed, although variability in both size and the ratio of slaves to slave-makers under natural conditions is much greater than that represented here. Previous research (Goodloe et al., 1987) showed that a *P. lucidus* raid on a host species other than the one already present in the nest is a rare event. Cool-Kwait & Topoff (1984) estimated that 75% of the brood retrieved by *P. lucidus* raiders is consumed. Considering the differential consumption of pupae according to species shown in this experiment, it seems unlikely that any pupae of a slave species, other than the resident one, would survive to eclose in a *P. lucidus* nest.

DISCUSSION

The first hypothesis concerning the origins of dulosis was Darwin's (1859) suggestion that slavery developed as a by-product of brood predation among related species. A second hypothesis (Wilson, 1971; Alloway, 1980; Stuart & Alloway, 1982; Topoff et al., 1984) focuses on territorial interactions, with opportunistic brood predation, as the main pathway to dulosis. Both hypotheses assume

Table 4. Consumption of pupae: same vs. alien slave species

Colony	# Slaves	#Raiders	Total F.N.* Pupae Consumed	Total F.S.** Pupae Consumed
P5A	100	25	15	3
P5B	100	12	33	0
P5C	100	25	32	2
P5D	100	50	12	0
P5E	100	100	35	3
S	200	0	33	2
Mean			26.667	1.667

* of 55 *F. nitidiventris* pupae

** of 55 *F. schaufussi* pupae

t = 5.24; df = 5; p < .005

that the interactions—either brood predation or territoriality—occurred between closely related species, which would increase the probability that captured brood might survive in the captors' nest.

Although Experiment 1 showed that unenslaved *F. schaufussi* colonies treat pupae from alien conspecific colonies as their own, no information was provided to determine whether the workers are able to discriminate such alien pupae from their own. Experiment 2, by contrast, showed that enslaved *F. schaufussi* workers consume large amounts of captured alien conspecific pupae. Since none of the colonies in Experiment 2 had larvae, and since colonies appeared to be satiated on the laboratory diet, consumption of protein-rich pupae is even more difficult to explain. Possibly in these slave-makers, unique dietary requirements led to brood predation in the ancestral slave-makers. It might seem equally parsimonious to assume that a previously established host-parasite association, possibly the result of territorial interactions, led to more specialized dietary needs in the slave-makers. However, in the *Neoformica* species enslaved by *P. lucidus*, and in the *F. fusca* group species enslaved by *P. breviceps*, considered (by way of Emery's Law) to be the closest relatives of these slave-makers (Wilson, 1971), there is no evidence to suggest a predisposition toward such territorial behaviors.

In Alloway's (1980) experiments with three *Leptothorax* slave species, both interspecific and intraspecific raids occurred. Some captured brood survived, resulting in both interspecific and intraspecific slavery. More important, however, were the findings from

queenright colonies in the field, where each of the three species contained several workers of one of the other species and no evidence of slave-makers. Subsequent brood produced by these colonies was of the same species as the queen and the majority of workers in the colony. This suggests that facultative slave-making occurs among species which are normally enslaved by other species.

For *Formica*, by contrast, no mixed colonies of these slave species have ever been reported in the absence of slave-makers. Laboratory manipulations with *F. schaufussi* and *F. nitidiventris* (in which two conspecific colonies are connected and no emigration is possible) have shown that colony fusions often occur, with relatively little violence, with the exception that at least one queen is usually eliminated (Goodloe & Topoff, unpublished data). Workers of the eliminated queen might be considered "enslaved" by the others, but there is no evidence that such fusions occur in nature. Admittedly, such conspecific mixes would be almost impossible to detect in the field.

While the *Leptothorax* territorial encounters were marked by continuous violence (Alloway, 1980), *Neoformica* colony fusions were characterized by a curious lack of aggression. Although initial encounters with alien conspecifics resulted in fighting, this behavior often disappeared within a day, and subsequent encounters were impossible to distinguish from encounters with nestmates. This lack of aggression is not consistent with traditional concepts of territorial behavior.

The lack of discrimination in the care of pupae from alien conspecific colonies in *F. schaufussi* and *F. gnava* is not surprising since extra conspecific workers can be absorbed into the service of the queen present in the nest and might provide an adaptive advantage. However, it is difficult to speculate on selection pressures that might exist when there are no known interactions between free-living colonies of these species that would result in one colony coming into possession of a conspecific colony's brood.

Differential consumption of brood of another species is consistent with developmental studies (Jaisson, 1975; Le Moli & Passetti, 1977; Le Moli & Mori, 1982) which show that some *Formica* species imprint, during the days following eclosion, to the brood present in the nest. After that time, they will care for the brood of the species to which they were exposed, and treat the brood of other species as food. In *Raptiformica* colonies, it is common to find more than one

species of slave present, and thus the slaves must accept pupae from more than one species. It would be interesting to track the fate of captured pupae from different species, with the species composition of several generations of slaves that had eclosed in the slave-makers nest.

Alloway (1982) speculated that the enhancement of pupae acceptance in *Leptothorax* slaves by the presence of the slave-makers is pheromonally mediated, with a substance either applied to the pupae themselves or transmitted trophallactically by the slave-makers. Possibly, the "deterioration" of pupae acceptance, or the switch to conspecific pupae as a food source by *F. schaufussi* in the presence of the slave-makers, is mediated the same way. As the above comparisons suggest, the evolution of dulosis has apparently proceeded along quite different pathways in myrmicine and formicine ants.

SUMMARY

Pupae acceptance behavior was studied in *Formica* species used as slaves by the slave-making ant genus *Polyergus*. Only one slave species is found in any single *Polyergus* nest. Pupae exchanges between different free-living colonies of *F. schaufussi* (enslaved by *P. lucidus*) and *F. gnava* (enslaved by *P. breviceps*) demonstrated that workers treat pupae of alien conspecific colonies as their own. However, in the presence of their slave makers, enslaved *F. schaufussi* workers consume a greater proportion of alien conspecific pupae than their free-living sisters. Also, enslaved *F. schaufussi* workers consume more pupae of a different slave species of *P. lucidus* (*F. nitidiventris*) than of the resident slave species. Comparisons with studies of pupae acceptance in slave species of myrmicine slave makers suggest they may have followed a different evolutionary pathway to dulosis.

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