BEHAVIOR OF THE SLAVE-MAKING ANT, *HARPAGOXENUS AMERICANUS* (EMERY), AND ITS HOST SPECIES UNDER "SEMINATURAL" LABORATORY CONDITIONS (HYMENOPTERA: FORMICIDAE)[1]

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Introduction

Slave-making ants are social parasites that raid the nests of host-species colonies, capture brood, and transport it back to the parasite colony. There, host-species workers eclosing from captured brood become "slaves" which perform all the usual worker-ant functions in the slave-maker colony (see review by Buschinger *et al.* 1980).

Harpagoxenus americanus (Emery) is an obligatory slave-making parasite which forms mixed colonies with workers of three *Leptothorax* host species: *L. ambiguus* Emery, *L. curvispinosus* Mayr, and *L. longispinosus* Roger. Young *H. americanus* queens found colonies by entering host-species nests, killing or driving off the adults, and inducing the host-species workers which subsequently mature from worker pupae in the nest to rear a brood of slave-maker workers (Wesson 1939). These parasite workers then augment the slave worker force by raiding other host-species nests.

Wesson (1939) and Alloway (1979) observed *H. americanus* slave raids in the laboratory by placing populous *H. americanus* nests in

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experimental arenas containing an arbitrarily selected host-species target nest. Under these circumstances, *H. americanus* raids begin when one or more slave-maker workers leave the parasite nest to explore the arena. Whenever such a "scout" discovers the entrance to the target nest, it returns to its own nest and recruits a raiding party. After dispersing the adult residents of the target nest, the raiders carry the captured brood back to the slave-maker nest (Alloway 1979).

Recently, it was discovered that *H. americanus, L. ambiguus, L. longispinosus* and probably *L. curvispinosus* form facultatively polydomous colonies (Alloway *et al.* 1982; Del Rio Pesado & Alloway 1983). Colonies of the three host species are also facultatively polygynous (Alloway *et al.* 1982). However, *H. americanus* colonies apparently never contain more than one inseminated egg-laying queen (Buschinger & Alloway 1977).

In the present paper, we augment previous findings by presenting behavioral observations of *H. americanus* and its slaves interacting with ants from other *H. americanus* colonies and from unenslaved host-species colonies. These observations supplement previous findings for three reasons:

1. The interactions observed were among ants from colonies collected adjacent to one another in nature.
2. The ants were observed for several weeks.
3. Ants from small and "weak", as well as populous and "strong", *H. americanus* and host-species colonies were observed.

Materials and Methods

Nests of *H. americanus, L. ambiguus,* and *L. longispinosus* were collected on the Erindale Campus of the University of Toronto, in Mississauga, Ontario. Since we wanted to observe the behavior of ants from parasite nests occurring close together in nature, we looked for places where there were at least two *H. americanus* nests within less than 2 m of each other. Whenever such a spot was found, we laid out a 2 m by 2 m quadrant centering on the parasite nests and then collected, numbered, and mapped the location of all *H. americanus* and host-species nests in the quadrant. Altogether, 19 quandrants were collected; but two pairs of adjacent quadrants were combined to permit observation of large groups of *H. americanus*

nests. See Del Rio Pesado (1983) for a complete demographic description of the colonies studied.

In the laboratory, the ants were removed from their natural nests, established in artificial nests (Alloway 1979), and censused. Then they were transported to a naturally lighted, unairconditioned room, where the field maps were used to reconstruct among the artificial nests the same spatial relations as had existed among the natural nests. In addition to these "natural" quadrants, we also observed one control quadrant containing two *H. americanus* nests from different collection sites. In some cases, individual ants were marked. See Del Rio Pesado and Alloway (1983) for a detailed description of these procedures.

Ad libitum behavioral observations were made 8 h a day, 5 days a week during June, July, and August. Five quadrants were observed in 1980; and 14 quadrants were observed in 1981. An assistant was employed during 1981 to permit more detailed behavioral observations.

Results

Raiding

The slave-makers raided or attempted to raid the nests of adjacent colonies. Most raided nests belonged to unparasitized *L. ambiguus* and *L. longispinosus* colonies. However, in the control quadrant and in the two "natural" quadrants containing more than one *H. americanus* colony, the slave-makers from one colony raided nests belonging to another parasite colony.

Alloway (1979) observed that the raiding behavior of *H. americanus* is not highly stereotyped even when ants from a single parasite nest are interacting with ants from a single target nest. In the present study in which the slave-makers were often interacting with ants from several naturally adjacent colonies, the results were so complex and variable that their complete presentation requires a separate description of the events in each quadrant. See Del Rio Pesado (1983) for such an account. Here we summarize those observations.

Much of the behavioral variability could be attributed to demographic variability. One demographic factor was the number of nests in each quadrant. The initial number of slave-maker nests in different quadrants ranged from 2 to 6, while the initial number of

host-species nests ranged from 0 to 17. This variablity in nest density is probably correlated with small-scale differences in the availability and suitability of natural nest sites. In addition, the history of slavery in a particular spot might affect nest density, since *H. americanus* colonies may destroy or drive away adjacent host-species colonies.

Another kind of demographic variability involved the number of nests occupied by single colonies. Some *H. americanus* and some host-species colonies were initially polydomous. In the laboratory, some initially polydomous colonies moved into a single nest (became monodomous) before any significant interactions with members of other colonies occurred; but others remained polydomous during behavioral interactions with ants from other colonies (Del Rio Pesado & Alloway 1983). To raid host-species nests successfully, *H. americanus* colonies must deploy raiding parties containing several *H. americanus* workers. In successful polydomous *H. americanus* colonies, the slaves made this possible by carrying all or almost all the parasite workers to a single nest before raiding began. While so doing, the slaves sometimes (but not always) moved the entire *H. americanus* colony into one nest. In other polydomous slave-maker colonies where the slaves failed to assemble the parasite workers in this way, many slave-makers were killed during uncoordinated attacks on target nests.

A third kind of demographic variability involved differing degrees of maturity among slave-maker colonies. When collected, some of our *H. americanus* colonies were incipient (*i.e.* initially contained only an *H. americanus* queen, some slaves, and a brood), while others already possessed slave-maker workers. Wesson (1939), studying ants from the east-central United States, found that *H. americanus* began to raid only after the overwintered *H. americanus* brood had matured. In contrast, overwintered parasite workers in our colonies from southern Ontario began to raid before all their overwintered brood had matured. As young *H. americanus* workers eclosed, they augmented the raiding forces of mature colonies and initiated raiding in incipient colonies. Thus, mature colonies could start raiding earlier and had the potential to raid longer than incipient colonies. In both incipient and mature colonies, first-year *H. americanus* workers were involved in all phases of raiding (*i.e.* scouting, attacking target nests, and transporting captured brood).

In this last respect, *H. americanus* apparently differs from the European *H. sublaevis* (Nylander), in which slave-makers in mature colonies do not begin to scout until their second year (Buschinger *et al.* 1980). We also observed an apparent effect of experience on scouting. On their first forays in the spring or after eclosion, scouts ventured only a short distance from their nest. The distance travelled became greater as the number of forays increased.

Alloway (1979) observed that *H. americanus* workers could scout either singly or in small groups. In the present study, only individual scouting was observed. Alloway (1979) also observed that, whenever a lone scout discovered the entrance to a target nest, it would return to its own nest and recruit a raiding party. However, in the present study, lone scouts sometimes attacked target nests by themselves. Nevertheless, lone *H. americanus* workers rarely, if ever, captured any brood. Invasion of a target nest by a single slave-maker excited the target-colony workers and often caused them to attack the intruder. Some lone intruders were killed.

The success of raider recruitment was highly variable. Upon entering its nest, a scout that had discovered the entrance to a target nest was immediately surrounded by a cluster of slave-makers and slaves. Shortly thereafter, the scout would make its way back to the nest entrance and leave. That the slave-maker was now almost certainly laying down a pheromone trail was indicated by the fact that it conspicuously dragged its gaster along the substrate while being closely followed by a column of other slave-makers and/or slaves. All scouts that had located target nests excited their nestmates; and most initiated processions. The variable success of raider recruitment seemed to depend on the "steadiness" of the recruiter's movement and orientation while leading the procession. Successful recruiters moved steadily forward without making any abrupt turns. Less successful recruiters stopped for prolonged periods and changed direction abruptly. Such hesitation caused nestmates to leave the procession; and badly disoriented scouts lost all their followers. Some initially unsuccessful individuals later relocated the target nest and went back to their nest to try again.

The arrival of a raiding party containing several *H. americanus* workers and (often) a number of slaves always caused "alarm" in the target nest. Workers and queens would snatch up larvae and pupae and make frenzied efforts to leave the nest. Whenever they found a

place where they could safely deposit any brood with which they had escaped, the workers returned to the invaded nest and carried off more brood. The slave-makers countered all these efforts by guarding the nest entrance (Alloway 1979) and by charging and snapping at target-nest workers.

Alloway (1979) observed that target-nest workers always fled with whatever brood they might manage to carry almost immediately after the arrival of a raiding party. In these circumstances, the slave-makers did not use their large, specialized mandibles against the residents of target nests. In the present study, a broader range of target-nest resistance and slave-maker aggression were observed. The workers in some target nests fled very shortly after the raiders arrived; and, in these cases, the slave-makers injured very few, if any, target-nest residents. However, in other target nests, the workers bit and stung the invaders. The slave-makers crushed such resistance by employing their large mandibles to dismember their adversaries. Slaves in raiding parties also attacked target-colony workers, but it was apparent that the success of the always outnumbered raiders depended mainly upon the activities of the slave-makers.

After all the adults had been killed or driven from the target nest, the raiders transported the captured brood to the slave-maker nest. Most brood was carried by slave-makers, although slaves sometimes carried one or two larvae or pupae. Brood transport generally lasted only a few hours, after which the raiding party vacated the target nest. Only one *H. americanus* colony manifested the phenomenon reported by Wesson (1939) of raiders requiring 2 or 3 days to complete brood transport. After the raiding party had abandoned the target nest, its previous inhabitants often returned.

Other Behavior

Our observations confirm that *Leptothorax* slaves do most of the work in *H. americanus* colonies. The slaves forage for food, feed and groom the parasite adults and brood, and defend the area around *H. americanus* colonies by attacking foraging workers from neighboring *Leptothorax* colonies whenever they are encountered near an *H. americanus* nest. The slave-makers do none of these things on a regular basis. Indeed, the parasites appear never to leave their nests except to scout (*i.e.* to "look for" target nests). Since scouting slave-makers invariably return to the same nest from which they departed, the parasites are even dependent on their slaves to

move them from nest to nest in polydomous colonies. Nevertheless, *H. americanus* workers possess certain vestiges of non-parasitic behavior. Inside their nest, *H. americanus* workers routinely groom one another, periodically share regurgitated food with other slave-makers and slaves, and occasionally engage in what appears to be brood care. Parasite workers may even eat if they encounter food while scouting. On such occasions, one can infer that the slave-maker is scouting (and not foraging) from the fact that, after eating, it continues to "look for" a target nest, instead of returning directly to its own nest, regurgitating to nestmates, and recruiting them to the food source. *H. americanus* workers never recruit or follow nestmates except in the context of slave raids.

Although *Leptothorax* slaves generally look after the slave-makers, we observed many instances of slave aggression against slave-makers. In 9 slave-maker colonies, we saw slaves biting and dragging *H. americanus* workers out of slave-maker nests. A few *H. americanus* workers lost parts of appendages as a result of these attacks. However, we never saw a slave-maker attack a slave; and we never witnessed anything resembling a generalized "slave revolt". Individual *H. americanus* workers were attacked by individual slaves. The same slave which attacked one slave-maker would feed and groom another; and any slave-maker that was attacked by one slave was cared for by others.

A somewhat different kind of slave aggresssion was seen in one of our incipient *H. americanus* colonies. When collected, this colony possessed a single nest containing an *H. americanus* queen, 17 *L. longispinosus* workers, and a brood. Throughout the course of our observations, the slaves fed and groomed the parasite queen and tended her brood through the pupal instar. However, the slaves killed all eclosing *H. americanus* workers. Similar events have been observed in other incipient *H. americanus* colonies (R. J. Stuart, personal communication).

As we have noted, slaves ordinarily defend the area surrounding *H. americanus* nests against incursions by unenslaved *Leptothorax* workers. Similarly, unenslaved *leptothorax* workers defend areas around their nests against incursions by *Leptothorax* slaves. These phenomena, together with the fact that both enslaved and unenslaved *Leptothorax* workers fight for their respective colonies during slave raids, indicate that enslaved and unenslaved *Leptothorax* workers generally recognize one another as belonging to different

colonies. However, these behavioral barriers between colonies are sometimes imperfect in the case of incipient slave-maker colonies. For example, let us consider the situation in Quadrant 3.

When collected, this quadrant contained two incipient *H. americanus* colonies, each of which was located near an apparently unparasitized *L. longispinosus* nest. In both cases, some of the slaves entered the nearest *L. longispinosus* nest without being attacked; and, reciprocally, some of the seemingly unenslaved *L. longispinosus* workers entered the *H. americanus* nest with impunity. On one occasion, a slave picked up the *H. americanus* queen in one of the parasite nests and carried her to the nearest *L. longispinosus* nest. The arrival of the parasite female caused all the adults in that nest to flee. Later the same day, a slave carried the *H. americanus* queen back to the nest from which she had come. Then, over a 12-day period, many of the workers which had originally fled moved in and began to live peacefully with the *H. americanus* queen in her nest.

Equally interesting events involved the other incipient parasite colony in the same quadrant. A slave which could peacefully enter the nearest *L. longispinosus* nest began to carry brood and workers from that nest into the *H. americanus* nest. Some of the in-coming *L. longispinosus* workers were accepted immediately by the other slaves, while others were initially attacked. However, after 15 days, all the workers from the unparasitized nest were living peacefully with the *H. americanus* queen. A few days later, several *L. longispinosus* workers killed the *L. longispinosus* queen which had been living in the unparasitized nest.

Discussion

Both Wesson (1939) and Alloway (1979) produced slave raids by selecting target nests and placing them in arenas with relatively populous, single-nest *H. americanus* colonies. The present study was the first in which a broader sample of *H. americanus* colonies has been observed and the first in which *H. americanus* colonies have been observed interacting with other colonies near which the slave-makers had been living in nature. These procedural differences probably account for the discrepencies between the behavioral events observed here and those described by Alloway (1979). Similar procedural differences, combined with possible regional differ-

ences between populations, may account for differences between the present results and those of Wesson (1939).

A number of our observations pertain to limits on the success of slave-raiding in polydomous parasite colonies. Individual *H. americanus* workers can rarely capture brood and are sometimes killed by target-colony workers. Yet, groups of 4 or 5 *H. americanus* workers can successfully raid almost any target nest. Thus, *H. americanus* colonies need to deploy their raiders in raiding parties containing several parasite workers. However, polydomy sometimes prevents such deployment. The slave-makers rely on their slaves to carry them from nest to nest in polydomous colonies; and the slaves often fail to assemble the slave-makers in a single nest from which successful raids could be mounted. As a consequence, some polydomous *H. americanus* colonies fail to organize raiding parties containing enough slave-makers to capture brood from neighboring host-species colonies.

This difficulty encountered by *H. americanus* colonies living in more than one nest has led us to question the adaptive value of polydomy in the slave-maker population studied. Both the *Leptothorax* host species enslaved by *H. americanus* in the Toronto region form facultatively polydomous colonies (Alloway *et al.* 1982). Thus, if enslaved host-species workers behave like unenslaved conspecifics, slaves should tend to provide a polydomous colony structure for the parasites. Perhaps, some *H. americanus* colonies are polydomous because of this behavioral propensity of their slaves and despite the fact that polydomy is detrimental to efficient raiding.

In addition, polydomy may account for some of the overt aggression observed in the present study. By extension, polydomy might partly explain the similar forms of slave aggression manifested by *Leptothorax* slaves living in *L. duloticus* colonies (Wilson 1975).

Let us imagine that a slave-maker colony divides, with some of the parasites and slaves remaining in the original nest, while others move to another nest. Let us further suppose that the slave-makers in the two nest raid independently. In such a situation, young slaves maturing from captured brood in each nest might learn to recognize as nestmates only those particular slave-makers with which they were living. If the ants from the two nests later reunited, then the old slaves might accept all the slave-makers, while the young slaves

accepted only familiar individuals. This scenario could explain our observations of slaves biting and dragging slave-makers out of nests. The aggression observed was always an individual matter. Some slaves accepted all the slave-makers, while other slaves accepted certain slave-makers and attacked others.

A somewhat similar hypothesis might account for the imperfect behavioral boundaries between some incipient *H. americanus* colonies and nearby unparasitized nests. An *H. americanus* queen founds a new colony by entering a host-species nest, killing or driving off the adults, and capturing worker pupae that subsequently mature to become her first slaves (Wesson 1939; Sturtevant 1927). If a parasite queen founded a colony in one nest of a polydomous *Leptothorax* colony, it would not be surprising if some of the parasite's first slaves were acceptable in other nests of the same colony. Similarly, "free" workers from that colony might be acceptable in the slave-maker nest. However, this hypothesis cannot explain how, under these circumstances, a parasitized nest could unidirectionally siphon brood and workers from an unparasitized nest or how an *H. americanus* queen could become more attractive than a *Leptothorax* queen. Yet, *H. americanus* queens and the queens of many other socially parasitic species somehow usurp the place of host-species queens (Wilson 1971). How parasite queens accomplish this feat remains an important subject for future research.

Polydomy also cannot account for the case where slaves cared for an *H. americanus* queen and her brood but killed all eclosing *H. americanus* workers. Explaining this phenomenon would require understanding the mechanisms of nestmate recognition in these species; and these mechanisms are incompletely understood. However, studies in progress (R.J. Stuart, personal communication) indicate that apparent "mistakes" in nestmate recognition are possible in these host species and that *H. americanus* may exploit these possibilities. When slaves work for a parasite queen, they may be mistakenly identifying her as a nestmate. When the same slaves destroy the parasite's offspring, they may be correctly identifying them as aliens.

Gladstone (1981) discussed various theoretical reasons why slave workers should not "revolt" against slave-makers. However, our observations of *H. americanus* colonies and Wilson's (1975) observations of *Leptothorax duloticus* colonies show that individual slaves sometimes manifest what might be interpreted as "rebellious behavior". If our inferences about polydomy are correct, whole

slave worker forces may even organize slave-maker colonies in a way which produces inefficient raiding. Nevertheless, we doubt that any of these behavioral phenomena are manifestations of evolved host-species defenses against slave-makers. We suppose that the behavior of host-species workers has evolved to maximize the reproductive potential of host-species queens. Slave-maker populations are so sparse that only a small proportion of host-species colonies are ever raided. Thus, slavery seems unlikely to exert significant selection pressure on host-species populations; and we believe that the facultative polydomy and polygyny found in these host-species are adaptations to conditions in host-species (not parasite) colonies.

In these host species, polygyny involves the acceptance of newly mated young queens in existing colonies. Simultaneously, polydomy involves a more or less continual exchange of workers, queens, and brood among nests; and such commerce requires workers in one nest to accept workers, queens, and brood from other nests of the same colony (Alloway *et al.* 1982). An incidental effect of these characterstics of host-species colonies is to produce a worker caste which is vulnerable to enslavement. Of course, a second effect of polydomy is to produce a worker caste which tends to organize multiple-nest colonies; and life in multiple nests may be disadvantageous to slave-makers. In other words, *Harpagoxenus americanus* parasitizes the labor of workers which possess a "mixed bag" of behavioral characteristics. Some of these characteristics may facilitate enslavement, while others may produce inefficient slave-maker colonies. However, the assertion that host-species workers have evolved to be inefficient slaves seems only a little more likely than the assertion that they have evolved to be slaves at all.

Summary

Colonies of the slave-making ant, *Harpagoxenus americanus* (Emery), and two of its host species (*Leptothorax ambiguus* Emery and *L. longispinosus* Roger) were observed under "seminatural" conditions, in which the ants lived in artificial nests arranged to reconstruct the spatial relationships among their natural nests. Some of the slave-maker and host-species colonies were polydomous,. In some polydomous slave-maker colonies, the slaves carried all the *H. americanus* workers into one nest before the onset of raiding. When thus assembled, the slave-makers efficiently captured

brood from nearby host-species colonies. In other polydomous colonies where the slave-makers remained in more than one nest, the parasites conducted unco-ordinated raids and incurred many casualties. Several kinds of slave aggression against the slave-makers are described. However, slaves "peacefully" augmented the slave worker forces of some incipient *H. americanus* colonies.

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