Strategies of Slave-making Ants and their Hosts

By LaniJo Kircher
lanijok@gmail.com

Abstract

There are several ant species that participate in slave-making, acting as parasites on other closely related species of ants. The slave-makers and their hosts have been shown to have coevolved in many different geographical areas. As would be expected, species of slave-making ants develop new tactics and specialties to raid the host’s nest more effectively and to most efficiently get slaves. As a counter defense, the host species develops new defense tactics, in attempt to keep the parasites from raiding their brood and to keep their colony alive. Different strategies are developed in different areas and for different host-parasite pairs. Many of the slave-making species have major and minor hosts reducing the coevolution between any two species in particular but increasing the need for evolution in both the parasite species and the host species. This paper covers the issues of coevolution between several slave-making ants and their respective host species. There is strong evidence for area specific coevolution as well as universal coevolution. There have been sites found that have both the most successful raiders and the most effective hosts at defending their colony. In areas where there is a strong parasitic pressure the host species has to keep up with the parasite species in terms of resistance. In many cases if a slave-making ant colony is exposed to a naïve source of host ants, that has never had parasites, the host species is better able to defend itself against these parasites. This shows that the slave-makers are adapted to their own local hosts and cannot make successful raids against this new species. Some adaptations discussed are
the development of cuticular hydrocarbon profiles that mimic the host species, manipulation of the host species using a substance secreted by the Dufour gland and behaviors during the raid. The host species are seen to have evolved resistant characters as well, including more guards at entrances, responses to Dufour secretions developed to decrease the impact of the secretion as well as changes in their life histories.

**Introduction**

One of the most common lifestyles of organisms on earth is parasitism. Parasitism is a type of symbiosis that involves a parasite species that uses a host species to enhance its life while causing harm to the host species in some way. Since the parasite species and host species have such interwoven lifecycles they often have very close evolutionary processes as well. The host species develops new resistances and the parasites develop new tactics to get around these resistances, and then the hosts have to develop new resistance. This reciprocal coevolution has been described by both the “arms race” and the “red queen” metaphors (Brandt and Foitzik, 2004). The basic idea in both of these hypotheses is that the two parts of the system keep up with each other so as far as function they stay in the same place. This can be applied to predator-prey systems, host-parasite systems as well as many others. While new adaptations are always being evolved neither part of the pair gets ahead for long because a co-adaptation is always close behind. Both species end up where they started in terms of how well they are adapted to getting the better edge on the other species.

One such parasite host pair can be seen in many ant species. There are thought to be at least six genre in ants that participate in a parasite system known as slave-making
ants. These six genre are: *Leptothorax, Strongylognathus, Harpagoxenus, Formica, Polyergus, and Rossomyrmex* (Regnier and Wilson, 1971). The ants that the slave-makers use as hosts are usually a closely related species, often another species of ants within the same genre as the parasite species (Foitzik, Fischer and Heinze, 2003). These slave-making ants are considered to be social exoparasites. They live in their own nests, but periodically make slave raids on other ant species to collect new slaves, who are the ones that do all the normal chores and functions around the colony for the slave-making ants (Foitzik, DeHeer, Hunjan and Herbers, 2001).

One of the common slave making ants is *Protomognathus americanus*. New *P. americanus* colonies are started when an already mated queen invades a host colony, which for the *P. americanus* is one of three species in the genre *Leptothorax*. The queen and the workers from the parasite colony either kill or drive out all the existing workers in the host colony and the host colony’s queen. They then settle into the colony and keep it as their own from then on. This colony starting slave raid is usually conducted in the mid to late summer when the host colony contains worker pupae (Foitzik, Herbers, 2000). When the host worker pupae emerge they begin to work for the parasite queen, care for her brood and begin taking care of all the normal ant colony tasks. The slave-maker workers that result from the parasite queen laying her own eggs do not participate in any of the normal colony chores. Instead they are specialized only for making periodic slave raids on nearby host colonies to replenish the force of slaves in the parasite colony (Blatrix and Herbers, 2003).

These replenishing slave raids are also carried out when the host colony has pupae in its colony. The slave-making ants invade the host colony and steal the worker brood
and take it back to their colony (Hare and Alloway, 2001). The adult ants that develop from the stolen brood then become the slave workers in the parasite colony, while the parasite colony’s workers continue to only participate in periodic raids to keep replenishing the slaves.

Since there are so many different ant species that participate in slave-making it is not surprising that there is also different levels of parasitism on the host species. Some species, like the *Formica subnuda* and *Formica sanguinea*, are facultative slave-makers. This means, that while they use slaves, they are not reliant on them. If slaves are not available, the workers in the parasite colony are capable of doing the colony work on their own. These facultative slave-making species have been found in the field both with and without slaves. There are some species though, such as *Formica subintegra* and *Leptothorax duloticus*, that are obligate slave-makers. These species cannot exist without slaves. They are found in the field only with slaves and in high proportions. Obligate slave-makers cannot successfully carry out the necessary colony tasks without the use of a slave species. When slaves were experimentally removed from *L. duloticus* the workers began to expand their behaviors, but they still never carried out many of the essential tasks such as carrying or handling insect prey which prohibited their survival without slaves (Savolainen, Deslippe, 2001).

**Discussion**

**Evidence for coevolution**

There are two competing hypotheses for the type of coevolution that exists between slave-making ants and their hosts. The two possibilities are universal
coevolution and localized coevolution. By the universal coevolution model there are a certain number of possible solutions to effective host and parasite strategies. Under this model, all populations are evolving universal adaptations and counter adaptations, but each population will be undergoing this evolution at its own rate. So while all populations are undergoing the same evolutionary process each parasite host pair population will be at a different level of adaptations. This model also predicts that if the best raiders are parasites from a particular site then the hosts from that site will also have the best defenses against the raids (Foitzik, DeHeer, Hunjan and Herbers, 2001). This follows along with the arms race hypothesis as well. The hosts that have the most parasitic pressure, which means the best parasites are in the area, will have the hosts with the most adaptations to counter the parasites. There is support for this model in studies that were done with Protomognathus americanus slave-makers and Leptothorax longispinosus hosts, comparing the raiding and defense abilities in two different sites, one in New York and one in Vermont. It was found that the ability to make successful raids was indeed countered by the ability of the hosts to successfully counter those raids. The New York site turned out to have both the most successful slave-maker parasites and the most successful defense strategies in the hosts (Foitzik, DeHeer, Hunjan and Herbers, 2001).

The other model is that of localized coevolution. This model states that each host and parasite population develops their own coevolution path that differs from any other sympatric-population pair. This model therefore predicts that there would be different strategies for each locale with little or no similarity between the geographical variation of populations (Foitzik, DeHeer, Hunjan and Herbers, 2001). There is no specific
relationship as to which strategies are better, just that they all develop separately. Support for this model lies mostly in that there are different strategies among the different species that participate in slave-making behaviors.

While there is support for both models and thus the issue of what type of coevolution is taking place, there is little argument that some sort of coevolution is indeed taking place between the slave-making ants and their hosts. An experiment was done to detect if there even was any sort of adaptation in the slave-making ants for their local hosts. When naïve host colonies (from a population in England unparasitized by any slave-maker ants) of *Leptothorax acervorum* were subjected to the slave-maker *Harpagoxenus sublaevis* they were actually shown to bite and sting the slave-makers more often and were better able to defend themselves fully from the parasites than were *H. sublaevis*’s normal host. This was explained by the fact that *H. sublaevis* was well adapted to its local host, and given a different host it was not able to make nearly as successful of a raid (Foitzik, Fischer and Heinze, 2003).

**Parasitic slave-making species**

One of the first things that it would seem that the slave-makers would run into would be how to get the slaves to work for their colony. It turns out that ants learn their colony odor in early adult hood during a sensitive phase (Brandt and Foitzik, 2004). The pupae that is stolen from the host species during the raids are unable to release themselves from their cocoons without help from workers. During the releasing process there is a lot of contact between the two species and exchange of trophallactic substances (Cougourdan, Provost, Riviere, Bagneres and Dusticier, 2004). It is thought that this and
other exposure in the first few days results in the slave ants accepting the parasite queen and colony as their own. This mechanism is supposed to make sure that the ants accept their relatives as their own colony, thus enhancing kin selection, but in this case it causes them to accept the parasite colony instead (Hare and Alloway, 2001).

It has been observed that colonies of slave-making ants are often composed of several different nests. Only one of these nests has a queen and the others are queenless. These colonies are formed by the raiders staying in the host colony instead of bringing the host pupae back to the queen. The frequency with which this occurs appears to be based on the availability of host ants on which to conduct raids. It has been shown that workers in nests containing queens produce little or no brood. In queenless nests the workers do, however, produce brood. The *Polyergus americanus* sites observed in West Virginia had little opportunities to raid hosts nests and as a result the queen monopolized reproduction and the colony existed mostly in one nest. In New York, on the other hand, there are lots of raiding opportunities and the workers often stay behind in the raided colonies. These multiple nest sites skew the dominance hierarchies in the colony as well as the sex ratios (Blatrix and Herbers, 2003).

It has already been shown that slave-making species of ants are best adapted for their local host species. One of these adaptations is the ability of the parasite species to mimic the cuticular hydrocarbon profile of their normal host. Though the species are usually closely related, the hydrocarbon profile is different. Thus the odors of the colony are different, which is one of the things that trigger aggression towards ants of a different species. Host species recognize their parasites by cuticular hydrocarbons and show high levels of aggressive-defensive behaviors towards them (Zamora-Munoz et al, 2003).
mimicking the cuticular hydrocarbon profile and odor of the host species it has been observed that *Harpagoxenus sublaevis* are able to sneak into host colonies without triggering any aggression (Foitzik, Fischer and Heinze, 2003). The ability to arrive in the host colony without triggering any aggression puts them that much closer to a successful raid.

During raids, in order to successfully steal the brood the slave-making ants must kill or expel the host colony workers so as to have access to the brood. An adaptation in *H. sublaevis* as well as some other species is a propaganda substance that it secretes from the Dufour gland. This substance induces aggression in the host species towards other members of their own colony, thus starting deadly fights among members of the host species (Foitzik, Fischer and Heinze, 2003). This allows *H. sublaevis* more flexibility in that it does not have to sting each host member directly but can apply the substance to the cuticle of members of the host colony and induce fighting. Along with inducing fighting among the slave species this substance has also been shown to enhance fear. When a crushed Dufour gland was placed in the midst of *Formica subsericea* they tended to scatter and retreat. Colonies of *F. subsericea* that had just been attacked by *F. subintegra* showed that most of the ants from the *F. subsericea* colony had been sprayed with large quantities of the propaganda substance from the slave-making species (Regnier and Wilson, 1971). Analysis of the propaganda substance shows that it is made up of a series of esters: decyl acetate, dodecyl acetate, and tetradecyl acetate (Regnier and Wilson, 1971). Some slave-making species carry up to 700 ug of this substance which is about 10 percent of an ant’s body weight. This substance apparently has other uses in the ant colonies. It is used as a defense mechanism against attackers of their own colonies and
also can serve as an effective alarm system for the ants (Regnier and Wilson, 1971). That this substance evolved in its use to include enhancing raiding behaviors makes sense. Both the effect of scattering and causing panic and that of colony fighting can be beneficial to the invading parasites. It takes care of part of the population of the host colony by simply spraying a few of the ants with the propaganda substance. With the host colony out of the way, or occupied in fighting each other, the slave-making ants can more easily get in to steal the brood.

**Host species resistances**

The impact of the slave-making ants on their host colonies is huge. It has been shown that in some populations the slave-making ants make as many as 5-11 raids in a year. This means that a given host colony has about a 50% chance of being raided (Brandt and Foitzik, 2004). These raids are usually very damaging to the colony, and the colonies often do not survive at all. Some studies done on *Leptothorax longispinosus* show that there are no local descendents left after a raid in the colony site. This implies that either the colony was forced to move to survive or they did in fact not survive the attack (Foikzik and Herbers, 2000). The defense strategies most likely do evolve from the parasitic pressures, but according to the evolutionary-lag hypothesis, they are always slightly behind and require time (Brandt and Foitzik, 2004). This means that due to needing sufficient time and genetic variation a host species can lag behind the adaptations of the parasite in terms of its ability to resist the attacks. There have been observations of several counter defenses developments by the host species as well including better
immunity to substances, better fighting abilities and colony guards, as well as the change in the ratio of sexuals in the colony.

When comparing the host populations of the ant *Leptothorax acervorum* with a population that was not plagued by parasites it was observed that the host populations placed a lot more guards at the entrance of their nests (Foitzik, Fischer and Heinze, 2003). This allowed for a quicker defense attack, as it didn’t allow slave-maker ants to make it very far into the host colony without being detected. The population that had never had parasites had no selective pressure for this type of behavior.

One big adaptation that is shown in a population of *L. acervorum* is the ability to resist the effects of the propaganda substance placed on them by the Dufour glands in their parasite species. It was experimentally shown that this species was not successfully manipulated by the Dufour secretions. Instead it was observed that host workers from this population often groomed the nest mates that had been treated with this secretion. This was presumed to be for the fast removal of the substance from the cuticle so that the worker was left unharmed (Foitzik, Fischer and Heinze, 2003). By removing the substance placed on them, they are able to get around the effects of the substance and are therefore better able to defend their colony.

Parasitic pressure also has an influence on the life histories of the host species. It was found that areas with high parasite pressure were correlated with the low allocation of workers in the host colonies and high allocation of sexuals as compared to areas with lower parasite pressure (Foitzik and Herbers, 2000). The lower number of workers protects against slave raids because there are less worker pupae for the slave-making ants to steal. Also with a higher number of sexuals the host colony has a better fitness return
and allows for dispersion of the colony to parasite free areas rather than just a growing colony where there are parasites.

**Conclusions**

Like most parasite-host systems, the slave-making ants and their hosts show many co-adaptations. While the parasitic species of ants are in many cases dependent on the host colonies and evolve many strategies to most successfully get slaves, the host species survival is in question as well and thus there is pressure for co-adaptations.
References:


