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Slave-making in ants, sometimes referred to as dulosis, is a form of social parasitism. The slave-makers conduct raids against neighboring colonies of other, related species, overwhelm the defending workers, and carry off their pupae and larger larvae. When the young captives eclose as adult workers, they accept the slave-makers as nestmates and join in the labor of the parasite colony. The workers of species in early stages of dulotic evolution are still relatively self-reliant. They assist their slaves in ordinary tasks and in some cases are able to survive without them. But those of the morphologically most advanced forms are completely helpless, having been transformed into specialized fighting machines capable only of conducting efficient slave raids.

Beyond its considerable intrinsic interest slavery in ants holds general significance for the study of behavioral evolution. Detailed comparison of slave-making species with closely related, free-living forms will identify the behavioral elements modified or lost during the early evolution of social parasitism, while the observation of the slave-makers with and without their slaves is a convenient means for revealing the amount of flexibility in the modified traits. For example, some behaviors are greatly attenuated or absent in slave-makers when the functions are filled by slaves. We may ask whether they will be evoked when the slaves are removed and survival demands a full, "normal" repertory.

Slavery has been discovered in six genera of ants: *Leptothorax, Harpagoxenus,* and *Strongylognathus* in the Myrmicinae; and *Formica, Polyergus,* and *Rossomyrmex* in the Formicinae (Huber, 1810; Kutter, 1969; Buschinger, 1970; Wilson, 1971*a*). Each of these taxa may contain at least one phyletic line that has evolved slavery independently of the others; it is at least safe to conclude that the habit originated three times, in *Leptothorax-Harpagoxenus, Srongylognathus,* and the Formicinae. *Leptothorax duloticus* represents a case of special interest. Its original discoverer, L. G. Wesson (1937, 1940), recognized that it represents an early stage in the evolution of dulosis. His observations on captive colonies revealed that although the species is an obligatory parasite on other *Leptothorax* (*L. curvispinosus, L. longispinosus*), its external morphology is only slightly modified and the organization of its slave raids are relatively crude. The behavior of *duloticus* has not been studied since Wesson's original work, partly because the species is rare and local. Wesson's type population appeared to be limited to an area of only about 100 square meters in an oak forest in Ohio. Subsequently Talbot (1957) discovered a more extensive population in the E. S. George Reserve of Michigan and subjected it to a demographic study, in the course of which she confirmed the obligatory nature of the dulosis.

In 1973, Dr. Talbot re-examined her study site and kindly supplied me with two queenright and four queenless mixed colonies of *L. duloticus* and its slave *L. curvispinosus* (see Fig. 1), together with unenslaved colonies of *L. curvispinosus* and the related species *L. ambiguus*. I took this unusual opportunity to make an intensive study of a rare and scientifically valuable species.

MATERIALS AND METHODS

To house the colonies, a method was invented that has proved remarkably success-

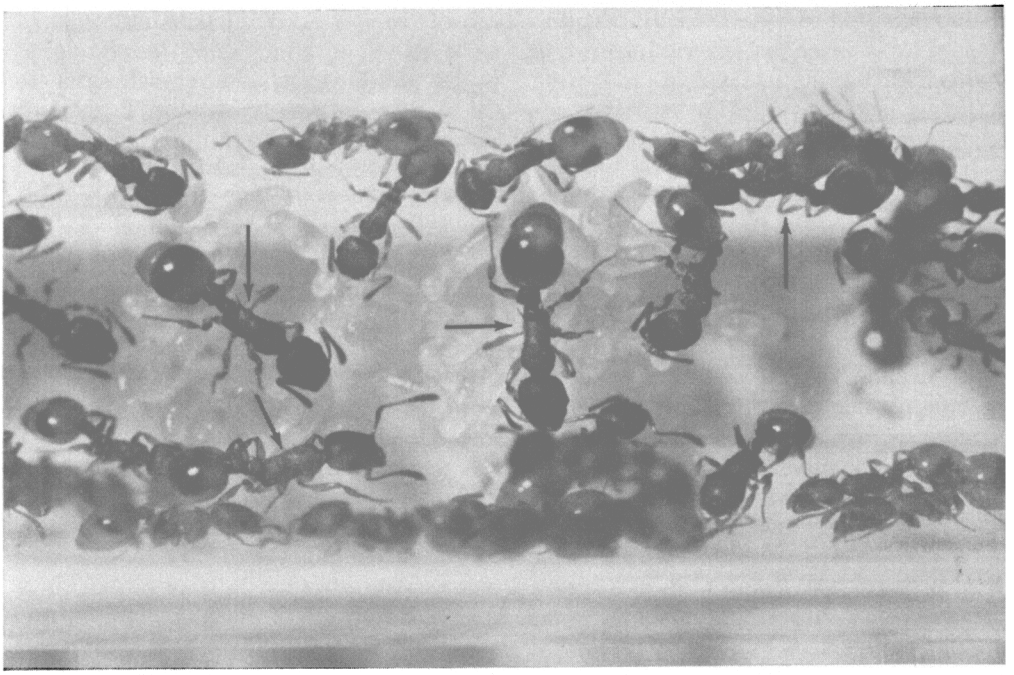

FIG. 1. A mixed colony of *Leptothorax duloticus* and its slave species *L. curvispinosus*. The four *L. duloticus* workers visible in this photograph are indicated by arrows.

ful with this and other small ant species. The ants are induced to move into a glass tube 10 cm long and 6 mm in internal diameter. One end of the tube is closed with a moistened plug of cotton wool which is in turn capped by a rubber or cork stopper to prevent rapid evaporation. The other end is left open, but the ants are provided with a small quantity of crumbled material from their original nest, with which they can close off the open end in a way that suits them. The tube is then placed inside a glass or plastic foraging dish about 12.5 cm in diameter and 6 cm deep. The inner walls are coated with fluon or plaster-of-paris dust to discourage climbing. Fresh honey and insect fragments are placed on the floor of the foraging dish every second day.

The whole ensemble, foraging dish and tube nest inside it, can be placed on the stage of a dissecting microscope and the full colony observed continuously. So long as they are within a tight enclosure such as the glass tube, *Leptothorax* colonies are relatively insensitive to light, and they will tolerate intense beams for indefinite periods during observation. A total of 51 hours was spent recording the behavior of the mixed colonies and 20 additional hours on unenslaved *curvispinosus* colonies. This is a relatively modest amount of absolute time compared to field studies of bird behavior, which occasionally occupy hundreds of hours, or primate behavior, a few of which have extended beyond 1000 hours. But it must be remembered that a colony of *Leptothorax* contains scores of individuals most of whose behavior consists of social interactions. The number of behavioral observations in this study is therefore comparable to that in many vertebrate studies.

ANATOMICAL DIFFERENCES

Phylogenetic relationships. The genus *Leptothorax* is large, diversified, and nearly worldwide. In order to judge the relation-

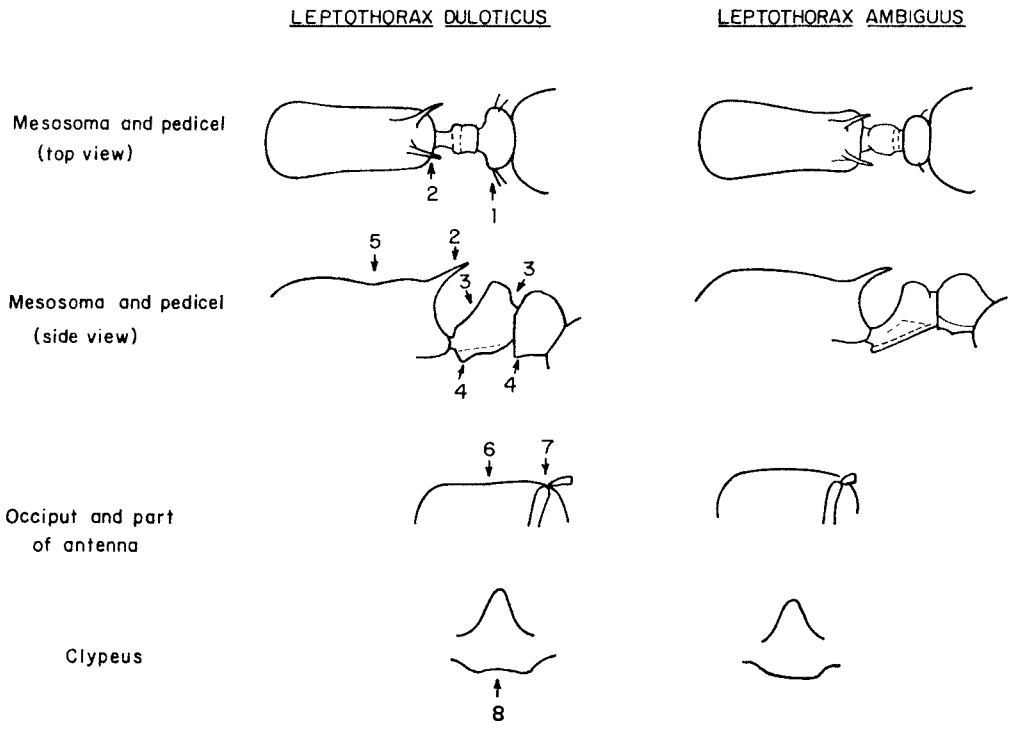

FIG. 2. Diagnostic traits in the external morphology of *L. duloticus*. The full combination of features indicated by the arrows distinguishes *duloticus* workers from those of *L. ambiguus*, the slave species most closely resembling it, and from other members of the *acervorum* group, although no single trait will suffice by itself. The traits are (1) broad postpetiole; (2) long, thick propodeal spines with blunt tips; (3) short, thick petiolar node with distinctive contour of anterior and posterior faces; (4) large subpetiolar and subpostpetiolar processes; (5) metanotal depression; (6) flat or feebly concave occipital border; (7) scape usually reaches or surpasses occipital corner; (8) anterior clypeal border feebly concave. *L. ambiguus* is also illustrated for comparison. Some of these features appear to facilitate slave-making behavior, as explained in the text.

ships of *duloticus*, I examined 97 other species in the genus representing every known species group and nearly all of the known North American and European forms. *Duloticus* is clearly a member of the Holarctic *acervorum* group, which is sometimes weakly separated as the subgenus *Mychothorax*. In external anatomy it most closely resembles *acervorum*, which is limited to Europe, and *muscorum* (= *canadensis*), the range of which is circumboreal and slightly overlaps that of *duloticus* at its southern limit. Both species are about equally close to *duloticus*, differing in details of sculpturing, pilosity, and contours of the thorax and pedicel. On the basis of distribution alone, the simplest hypothesis is that *duloticus* originated from an outlier population of *muscorum* or a free-living species that was cognate with it.

External morphology. Some of the diagnostic characteristics of *L. duloticus* are presented in Figure 2. A comparison has been made in this illustration with *L. ambiguus*, a slave species that resembles it superficially to a degree that makes identification in the field difficult. Observations of workers during slave raids have led me to believe that some of the diagnostic traits represent either preadaptations favoring a life of slave-making, adaptive modifications that appeared in conjunction with slave-making, or the former enhanced by the latter. In particular, it can be

hypothesized that the concavity of the anterior clypeal border aids in the carrying of large larvae and pupae from raided colonies. The *duloticus* workers, after fighting their way into the nest, seize the larvae and pupae with their mandibles and press the captives back against the anterior clypeal border. Brood carrying by the *duloticus* is basically the same as in other *Leptothorax* but differs in the behavioral specialization of the workers for carrying large pieces of brood, plus the fact that the transport must be conducted swiftly, in alien terrain, and under conditions of stress. These circumstances seem to favor the evolution of the contour of the mouthparts and the adjoining clypeus to provide a tighter fit of large objects. It is probably significant that a concave anterior border also distinguishes most of the slave-making species of the ant genus *Formica*. However, the trait is also shared with at least some of the free-living members of the *acervorum* group, including *muscorum*, and it is therefore best interpreted as preadaptive.

It was noticed during the raids that the *duloticus* workers were forced to extend their antennae at maximum length in order to reach around the piece of brood they carried and thus to continue testing the ground ahead of them. Under conditions of haste and stress, there should be a considerable advantage to longer antennal length, which in fact the *duloticus* possess (Fig. 2). Since this trait distinguishes *duloticus* from both *acervorum* and *muscorum*, it is quite possibly postadaptive with reference to slave-making behavior. Much of the fighting consists of dragging contests, during which the *duloticus* workers seize workers of the attacked colony and attempt to pull them away from the brood piles, exposing the latter to pilfering. The greater size of the slave-maker workers gives them a clear advantage in these contests. Finally, I hypothesize that the greater thickness of the petiole and postpetiole give an edge during combat. Ants often bite this part of the anatomy, which comprises the narrow "waist" of the body. A superior purchase can be gained there, and sometimes the opponent can be cut in two. The thicker and shorter segments of the *duloticus* workers, combined with their greater size, make this mode of assault less easy. This trait is more developed in *duloticus* than in *muscorum* and other free-living members of the species group, and it can be tentatively interpreted as postadaptive.

Ergatogynes. A mixed, queenless colony of *duloticus* and *curvispinosus* collected on 21 June, 1973, by Mary Talbot at the E. S. George Reserve contained, in addition to workers of both species, two ergatogynes of *duloticus*. These individuals are the first recorded for this species. The individuals lie at the upper limit of the size range of the worker caste but differ externally from ordinary workers only in the possession of well-developed ocelli, usually a trait of queens. The abdomen of each was found to be filled with a large ovary consisting of at least five ovarioles bearing eggs at various stages of development. Workers of *duloticus* and *curvispinosus* also possess functional ovaries, but they are much smaller and consist of only two or three ovarioles. The presence of ergatogynes is a frequent trait of parasitic ants, but it occurs sporadically in only a tiny minority of free-living species, including some *Leptothorax* (Buschinger, 1970; Wilson, 1971*a*). It is possible that the *duloticus* ergatogynes serve as reproductives in some of the numerous queenless colony fragments occurring in nature (see Talbot, 1957) and thus could be the progenitrices of entire new colonies.

Exocrine glands. Regnier and Wilson (1971) found that the Dufour's gland of the slave-making ant *Formica subintegra* is greatly hypertrophied and contains large quantities of decyl, dodecyl, and tetradecyl acetates, substances previously unreported in the formicine ants. They demonstrated that the esters are sprayed at defending workers during slave raids and act as "propaganda substances": while slowly dissipating, the substances strongly attract

the slave-makers but alarm and scatter the defenders. The exocrine morphology and chemistry of parasitic ants is therefore of considerable potential interest. During the present study, *Leptothorax duloticus* workers and ergatogynes were found to have Dufour's glands comparable or somewhat larger in size to those of *L. ambiguus* and *L. curvispinosus* and poison glands and reservoirs considerably larger (Fig. 3).

Freshly dissected poison glands and Dufour's glands were separated and variously crushed and streaked into artificial trails in the presence of free-living *curvispinosus* and mixed *curvispinosus-duloticus* colonies. The only response observed was a mild and short-lived excitement, much less intense than the response to volatile alarm substances located in the heads of *curvispinosus* workers. Thus no evidence was obtained that the two abdominal glands contain pheromones, at least any employed during slave raiding. It is equally possible that the larger poison gland apparatus merely provides a greater quantity of venom during combat. Since no workers of other members of the *acervorum* group have been dissected, it is not known whether the larger poison gland size of *duloticus* (compared with the slave species) represents a phylogenetically derived condition.

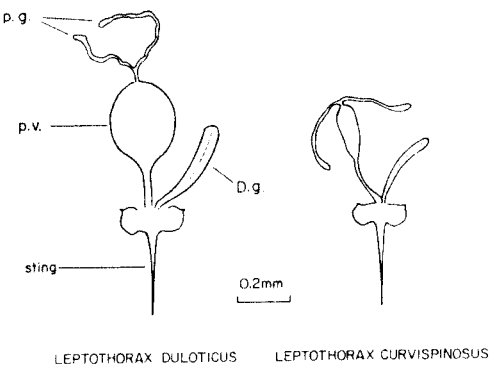

FIG. 3. The exocrine glands associated with the sting in workers of the slave-maker *L. duloticus* and its slave *L. curvispinosus*. The paired poison glands (*p.g.*) and the vesicle (*p.v.*) to which they are attached are proportionately larger in *duloticus*. The Dufour's gland (*D.g.*) is comparable in size or somewhat larger.

BEHAVIOR WITH AND WITHOUT SLAVES

In order to compare the behavior of *duloticus* with that of its slave species, and hence the division of labor between them, a mixed colony was observed for 51 hours over a six-weeks-long period, a catalog of all behavioral acts inside and outside the nest was prepared, and the relative frequencies of the behavioral acts were recorded. During this time the colony contained a single queen, 6 to 9 workers, and 2 males of *duloticus*; 12 to 20 *curvispinosus* workers; *duloticus* brood in all stages of development; and pupae and large larvae of *curvispinosus* captured in slave raids. Next the slaves were removed and placed in a separate nest and the now pure *duloticus* colony observed for seven hours over 6 days to detect behavioral changes induced by forced independence. Finally, the slaves were returned to the *duloticus* and the observations continued. Separate, less detailed studies were conducted on a second queenright mixed colony and several queenless mixed colony fragments.

The quantitative results are presented in Table 1. The main conclusions based on both the data and other, non-quantified observations can be summarized as follows.

Slaves present. When the *curvispinosus* slaves were present, they dominated positions in and around the queen and brood. To measure the difference, the three workers closest to the queen (and hence the egg piles) were identified to species at random intervals over a period of several weeks. Of 132 such identifications 119, or 90%, were *curvispinosus*. The *duloticus* were not simply removed from the queen and brood; they remained concentrated near the nest entrance (from which they mounted raids when *curvispinosus* colonies were supplied nearby). When workers within 2 cm of the nest entrance were identified at random intervals, 62 of 87 individuals, or 71 percent, were *duloticus*.

In spite of the difference in their location, the behavioral repertory of the *du-*

TABLE 1. *Relative frequencies of behavioral acts by the slave-making ant* Leptothorax duloticus *and its slave* L. curvispinosus, *in mixed colonies and alone.* N, *total number of behavioral acts recorded in each column.*

	Frequency of behavioral acts					
	L. duloticus			*L. curvispinosus*		
Behavioral act	Workers: in mixed colony ($N = 382$)	Workers: without slaves ($N = 401$)	Queen: in mixed colony ($N = 122$)	Workers: enslaved ($N = 1057$)	Workers: free-living ($N = 905$)	Queen: free-living ($N = 62$)
Self-grooming	0.2723	0.3342	0.1885	0.2081	0.2707	0.1290
Antennal tipping	0.0052	0.0056	0	0.0076	0.0177	0
Allogroom adult:						
duloticus worker	0.0419	0.0249	0	0.0104	—	—
duloticus queen	0.0052	0.0050	0	0.0019	—	—
curvispinosus worker	0.1728	—	0.0082	0.0416	0.0320	0
curvispinosus queen	—	—	—	—	0.0033	—
Brood care:						
Carry egg	0.0079	0.0374	0.0574	0.0132	0.0177	0
Lick egg	0.0157	0.0324	0.3279	0.0322	0.0177	0.0645
Carry larva	0.0210	0.0923	0.0164	0.1060	0.1503	0.0161
Lick larva	0.1047	0.2219	0.2377	0.1608	0.2033	0.4355
Assist larval ecdysis	0	0	0	0.0076	0.0033	0
Feed larva solid food	0	0.0175	0	0.0303	0.0376	0
Carry pupa	0.0131	0	0	0.0114	0.0132	0
Lick pupa	0.1545	0.0200	0.0410	0.0691	0.0243	0
Assist eclosion of adult	0	0.0025	0	0.0066	0.0099	0
Lay egg	0	0	0.0410	0.0038	0.0011	0
Regurgitate:						
With larva	0.0262	0.0499	0.0820	0.0795	0.0751	0.3548
To *duloticus* worker	0.0079	0.0224	—	0.0378	—	—
To *duloticus* queen	0.0236	0.0200	—	0.0170	—	—
To *curvispinosus* worker	0.0262	—	0	0.0426	0.0442	0
To *curvispinosus* queen	—	—	—	—	0.0099	—
Fight other workers	0.0052	0.0075	0	0.0161	0	0
Attack queen	0	0	—	0.0009	0	—
Lick wall of nest	0.0314	0.0249	0	0.0132	0.0144	0
Forage	0.0393	0.0274	0	0.0369	0.0199	0
Feed on honey	0	0.0100	0	0.0085	0.0022	0
Feed on solid food	0	0.0175	0	0.0199	0.0144	0
Carry dead insect	0.0026	0	0	0.0019	0.0033	0
Carry dead nestmate	0.0131	0.0050	0	0.0019	0.0033	0
Carry live nestmate	0	0.0025	0	0.0009	0.0022	0
Handle nest material	0.0026	0.0075	0	0.0019	0.0066	0
Stridulate	0.0079	0.0125	0	0.0095	0.0022	0
Totals	1.0	1.0	1.0	1.0	1.0	1.0

loticus workers was surprisingly lengthy and "normal" in appearance, confirming the impression that the species has not degenerated as much as such advanced slave makers as the species of *Polyergus*. Important differences nevertheless exist. The *duloticus* donated as well as received during regurgitation, but with much less frequency. *Curvispinosus* workers were seen regurgitating to *duloticus* workers on 40 occasions, but the opposite donation was recorded only 10 times. *Curvispinosus* donated to other *curvispinosus* 46 times, while *duloticus* gave to *duloticus* only on 10 occasions. At first glance this selfish tendency seems to be reversed in the pattern of allogrooming. While *curvispinosus* groomed *duloticus* 11 times and other *curvispinosus* 44 times, *duloticus* groomed *curvispinosus* on 66 occasions and other

duloticus 16 times; the difference is magnified by the fact that the *duloticus* were outnumbered by the slave species two to one. Furthermore, *duloticus* paid inordinate attention to pupae when they visited the brood: they were observed licking pupae 59 times, not much less than the 73 times the behavior was performed by *curvispinosus* workers, the principal nurses of the mixed colony. In contrast, *curvispinosus* licked larvae 170 times and carried them 112 times during the observation period, while the counts for *duloticus* were only 40 and 8 respectively. Clearly, then, the *duloticus* show an unusual preference for pupae. It is conceivable, but not yet supported by independent evidence, that the slave-makers obtain nutritive materials in the surface secretions of pupae and other workers.

It is certainly true that the *duloticus* workers paid little attention to other sources of food. Honey and insect fragments that were eagerly gathered by the *curvispinosus* slaves were ignored by the slave-makers. The *duloticus* also paid no attention to the shed skins of larvae and pupae, which were manipulated, eaten, and fed to larvae by the *curvispinosus* workers until totally consumed. In fact, with the exception of allogrooming, which we have just seen might be a selfish form of feeding behavior, and regurgitation with larvae, which might have been directed from the larvae to the *duloticus* rather than the reverse, the slave makers failed to function as nurses.

The *duloticus* were at least as equally efficient as the slaves in transporting brood to new nest sites when the colony was disturbed. Because this behavior consists of essentially the same elements as the transport of captured brood during slave raids, its full retention by the *duloticus* is not surprising.

Slaves absent. When the *curvispinosus* slaves were taken away, the repertory of the *duloticus* expanded dramatically. As seen in Table 1, the relative frequencies of acts shifted and entire behaviors appeared for the first time. The workers moved away from the nest entrance and other positions and concentrated on the brood. The eggs and larvae were now attended much more intensively. When the *duloticus* had slaves, they were seen to lick larvae on 40 occasions during 51 hours of observation; after the slaves were removed, the *duloticus* licked larvae on 89 occasions during only 7 hours of observation. The workers also began to feed the larvae solid materials. On 7 occasions they placed collapsed eggs and shed larvae or pupal skins on the mouthparts of the larvae.

The *duloticus* workers were clearly inept at assisting the ecdysis of brood. Several larvae and pupae were noted sitting with partly shed skins for many hours—something never permitted by the *curvispinosus* slaves when they were in charge of the brood. Yet in one instance a *duloticus* worker was seen to assist the emergence of another worker by stripping off pieces of pupal integument. A lack of competence also characterized nest-building behavior. Workers carried pieces of nesting material around in their mandibles but did not succeed in placing them together to form a plug at the nest entrance.

The slaveless *duloticus* began to feed on honey supplied just outside the nest entrance, a response they never showed when slaves were present. However, the feeding sessions were inordinately long, often lasting thirty minutes or more before the worker returned to the nest in a replete condition and began to regurgitate to her companions. Comparable episodes in *curvispinosus* took no more than five minutes. The one behavior that was never displayed by the *duloticus* workers, either with or without their slaves, was the retrieval and handling of insect prey. The slaveless workers were repeatedly offered a variety of newly killed insects, including five species of moths in several families, leafhoppers, flies, and a lacewing. The prey were given whole and chopped up into "hamburger," the latter conditions providing small pieces that could have been simply

picked up by the *duloticus* and carried without much effort back into the nest. Yet the only reaction observed was an initial mild interest followed by avoidance. Evidently the *duloticus* depend completely on nestmates to supply food and have completely lost the ability to hunt and to scavenge for insects outside the nest.

Slaves restored. When the slaves were returned, they quickly displaced the *duloticus* in the brood area, and the earlier patterns of activity and division of labor were resumed.

Slave Raids

Wesson (1937, 1940) induced raiding in captive colonies of *duloticus* and found the procedure to be slow and unorganized in comparison with the morphologically more specialized slave-making ants such as *Harpagoxenus* and *Polyergus*. Solitary scouts returned home after discovering a free-living colony of the slave species. They might or might not have captured a pupa before doing so, but in either case their arrival excited their sister workers and the resident slaves. Some of the latter then departed and began searching on their own. Wesson saw one initial scout return to the newly discovered nest, dragging its abdomen and apparently laying down a pheromone trail. She was followed by a procession of 18 *duloticus* and 5 or 6 *curvispinosus* slaves. The raiders fought their way into the colony, gradually overpowered the defending workers, and removed the brood. The process took about one hour, but the *duloticus* workers sometimes remained in the captured nest for hours or days afterwards.

The three raids I witnessed were similar to those described by Wesson, although no cases of trail-laying were seen and I was unable to induce following of artificial trails made from abdominal glands and other organs. *Duloticus* workers often stridulated upon returning to the nest with captured brood, especially when others took their captives from them. Stridulation also occurred when workers were fighting, either during raids or on other occasions, and during a small percentage of regurgitation bouts within the nest. Thus the communicative functions of stridulation, if any exist, depend on the context in which the act is performed. The *duloticus* workers were always more excited than their slaves by the return of a successful scout. In each instance, all became active, and most left the nest in searches of their own before the first *curvispinosus* workers began to exit. Curiously, the *duloticus* queen also became excited. She ran back and forth to the nest entrance but did not leave or join in the transport of captured brood within the nest itself. The first *duloticus* to encounter the target colony were comparatively timid and sometimes backed off or even ran away if confronted by a *curvispinosus* defender. But as excitement increased, the raiders began to attack without hesitation. The *curvispinosus* defended their brood stoutly, showing little of the panicked response often displayed during raids by the victims of *Harpagoxenus americanus*, or by species of *Formica* under attack from *F. subintegra* (see Wesson, 1939; and Wilson and Regnier, 1971). The favorite maneuver of the *duloticus*, apparently not observed by Wesson, was to seize the defender by an appendage or part of the body, drag or carry it away to the edge of the nest area, and dump it unharmed. The *duloticus* worker then rushed back into the nest and seized a piece of brood or, if necessary, fought with other defenders. In addition, *duloticus* workers grappled with defenders and stung them. Fighting by the *curvispinosus*, both the defenders and the janissaries who accompanied their *duloticus* mistresses, consisted primarily of grappling and stinging. The dumping technique was made easier by the typically greater size of the *duloticus*, and it was notably quicker and more efficient than more conventional fighting.

Facultative Slave and Slave-Making Behavior

Among the conditions that might favor the origin of slavery in ants are certain

behavioral predispositions in both the candidate slave-maker species and the candidate slaves. This hypothesis can be tested by answering the following question: do conditions exist under which colonies of ordinarily non-dulotic species raid each other and kidnap brood? This idea is not at all far-fetched. Kutter (1957) found that when colonies of *Formica naefi*, a European member of the non-dulotic *exsecta* group, are placed near colonies of members of the *F. fusca* group, they attack them and carry away the brood. The behavior has not yet been observed in undisturbed populations. Kutter noted that all larger *naefi* nests contain a few *fusca*-group workers, but this condition could equally well stem from the habit of *naefi* queens of founding colonies by invading *fusca* nests.

In order to test the propensities of *Leptothorax curvispinosus* workers, I placed a tube nest containing a small queenright colony next to a second nest containing a much larger colony. Workers of the second colony soon discovered and attacked their smaller neighbor in a manner quite similar to the raids of *duloticus*. They killed some of the workers and drove away the remainder along with the queen. Simultaneously they carried most of the brood into their own nest. The fate of the eggs and larvae could not be followed, but the *curvispinosus* workers allowed the captive pupae to eclose, and the young workers were adopted into the colony. This result establishes two points of interest. First, the raiding behavior of *duloticus* is fundamentally similar to the territorial behavior of *curvispinosus* and could be evolutionarily derived from something like it in the hypothetical ancestral species. Second, the fact that the adoption occurred shows not only that *curvispinosus* has certain prerequisite qualities for a candidate slave-making species, but also that it has the one requisite quality to be a slave species. For if captured brood were not adopted by *curvispinosus*, the population of *curvispinosus* could not be built up in the mixed colonies. The first slaves captured by the *duloticus* would instead execute all the others captured in later raids.

In order to learn whether the same propensities occur in interactions of free-living species, as opposed to interactions within species, the experiment just described was repeated four times, but with small *curvispinosus* colonies being placed next to large *ambiguus* colonies. In two cases, limited fighting occurred outside the nests but the colonies coexisted for a period of at least a week, at the end of which time the experiment was terminated. In the remaining two replicates, fighting led to raids and the ejection of the *curvispinosus* colony in a manner resembling that seen during the interaction between the two *curvispinosus* colonies. The *ambiguus* carried the *curvispinosus* brood into their own nests. The pupae were cared for and assisted during eclosion. The newly emerged *curvispinosus* workers were at first licked and treated like sister workers. But after one to several hours they began to be attacked, and within one or two days they were dragged out of the nest and killed. No *curvispinosus* worker was permanently adopted. Even so, the behavior of *ambiguus*, a typical free-living *Leptothorax*, is seen to be but one short step away from an elementary form of dulosis.

Aggression and "Revolt" within Colonies

A surprising amount of aggression was seen within the mixed colonies, both between the *duloticus* and their slaves and among the *duloticus* themselves. These observations are relevant to evolutionary interpretation in that they could be a reflection of a relatively imperfect degree of adaptation on the part of *duloticus* to a life of slave-making. Several instances of apparent hostility to the queen *duloticus* by slave workers were noted. The queen ordinarily maintained a form of dominance in the vicinity of the egg pile. As she moved about, *curvispinosus* workers making antennal contact with her head typi-

cally turned away or even fled to another part of the nest. *Duloticus* workers occasionally showed the same response to a lesser degree. This repelling influence is not unique to the queen of *duloticus*. In a later report I will show that it is strongly developed in interactions between *curvispinosus* workers and queens in unenslaved colonies and appears to serve the function of keeping a clear field for the queen as she feeds on secretions from the eggs and larvae. In other words, the aversion is evidently one additional form of altruistic behavior by workers and not subordination within a vertebrate-like dominance system. However, on several occasions *curvispinosus* workers transgressed the relationship in a way that can only be construed as hostile to the *duloticus* queen. Three times *curvispinosus* were observed to approach the queen on the egg pile and to bite at her head or thorax. Simultaneously or immediately afterwards the worker laid an egg. In two of the incidents the worker safely placed the egg in one of the egg piles; but in the third case the queen seized the egg, pulled it back and forth with the worker holding on to the other end, and finally ruptured and ate it. On still another occasion a *curvispinosus* worker laid an egg while away from the queen and inserted it into the egg pile without direct conflict.

Slave hostility was not limited to the moment of oviposition. Once, as the *duloticus* queen wandered away from the egg pile, she was seized on the right hind tarsus by a young *curvispinosus* slave, who then alternately tried to drag her backward and to sting her. From time to time during this incident, which lasted 20 minutes, the worker stridulated. All such actions are typical of *curvispinosus* workers engaged in fighting alien ants; they do not resemble in any way the initiation of transport behavior.

Similar attacks were conducted from time to time by various *curvispinosus* workers on both *curvispinosus* and *duloticus* nestmates. Some of the episodes were vigorous and prolonged, but they were all one-sided and never ended fatally. Hostility was especially pronounced after the slaves had been removed from the *duloticus* colony for five days and then returned. Four of the *duloticus* workers were immediately attacked by slaves and pinned down and dragged about for hours on end. After four days two workers were still being harassed. None of the episodes ended fatally, and the *duloticus* were never seen to fight back. Although the intensification of aggression by the slaves against the *duloticus* following separation can be explained by either a change in colony odor or weakening of odor memory, the original aggressive acts prior to separation cannot be explained in this way.

Even more surprisingly, the *duloticus* workers began to show hostility toward each other when deprived of both their queen and slaves. The commonest reaction was for one individual to rush at the head or thorax of another, antennating it vigorously and pawing it with the fore tarsi, then standing quietly but firmly on top of it. On other occasions workers seized others by the antennae or mandibles and dragged them backwards. When the slaves were returned (but not the queen, who had died), two more instances of light aggression were witnessed during the first day. Thereafter no such acts were observed. This set of observations may be unique. I know of no other instances of sister ant workers fighting among each other without either prior separation or some severe outside disturbance such as the artificial alteration of colony odor.

Discussion

The present study has revealed how remarkably few differences separate at least some (and probably many) free-living ant species from a slave-making existence. Only two relatively slight quantitative changes in the behavior of *Leptothorax ambiguus* and *L. curvispinosus* would be required to turn them into facultative slave makers. First, the tolerance toward adult captives

of other species would have to be increased. Instead of accepting newly eclosed adults for a few hours (the case in *ambiguus*), tolerance would have to be extended for days or even the lifetime of the captives. Second, the raiding distance would have to be increased to encompass not just adjacent nests but those as much as a meter or more away. Both of these modifications involve quantitative changes in the response thresholds of existing behavior patterns. It is possible that given the right selective pressures, they might occur in a few tens of generations.

To pass from facultative to obligatory slave-making is a more drastic step. Now the range of the species would be altered to fit within those of the slave species, and its population densities reduced or held to lower levels merely by the necessity to "harvest" continuously from surrounding host colonies. The obligatory state of dulosis implies some degree of behavioral decay in the slave-maker. We have seen that *L. duloticus*, while primitive in most respects, has a fatal inability to collect and handle insect prey on its own. It also demonstrates varying degrees of incompetence in nest building and the assistance of larval and pupal ecdysis. The loss of behavior is not difficult to achieve, however. A single gene can block a behavioral pattern, and the loss or severe reduction of behavioral elements has occurred in laboratory populations of *Drosophila* and *Peromyscus* field mice on the order of ten generations (see review in Wilson, 1971*b*). It is interesting to compare the disabilities of *L. duloticus* with the behavioral decay observed in other partially evolved social parasites. The workers of *Kyidris yaleogyna*, a Papuan species that lives in primitively xenobiotic association with *Strumigenys loriae*, are relatively ineffectual as brood nurses. They capture a few prey but are far less active and efficient in this role than the host workers. In the single study conducted, they were never observed to contribute to nest construction (Wilson and Brown, 1956). The European slave maker *Strongylognathus huberi*, a derivative of the genus *Tetramorium*, has a pattern of decay closer to that of *L. duloticus*. Besides conducting raids, the workers participate in raids and are able to feed themselves. But they neither hunt nor care for the brood (Kutter, 1969). It is possible that slave-deprivation experiments of the kind reported here for *L. duloticus* would reveal a wider repertory in both species. In most other dulotic and inquilinous ant species that still possess a worker caste, the workers have evidently lost the ability to conduct the ordinary functions of nest construction, food gathering, and queen and brood care.

The results of this study have shown how much preadaptation toward slave-making exists in at least one large genus of ants (*Leptothorax*) and how simple and few the steps are from the free-living state to the obligatorily parasitic state. Why is it, then, that such a tiny fraction of species are dulotic and all of these so far as known are limited to the north temperate zone? This is a question for which we do not yet have an answer. I doubt if the clue exists in present knowledge; it will probably turn up when deeper investigations of dulosis are pressed in the future.

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Summary

The little myrmicine ant *Leptothorax duloticus*, a rare and local species known from Ohio and Michigan, practices a primitive version of slave-making and provides an unusual opportunity for investigation of the evolutionary origin of this form of social parasitism. The most likely ancestor

or cognate species is the free-living, circumboreal *L. muscorum*. A few anatomical traits of *L. duloticus* are advantageous to the practice of slave-making. Some appear to be preadaptive, shared with free-living members of the same species group, others postadaptive, having been acquired after divergence from the nearest living relatives presumably as part of the shift to parasitism.

Behavioral decay is only slightly advanced. Although *duloticus* workers are less than competent in some types of behavior, such as nest-building and brood care, only one category, the gathering and handling of solid food, appears to have been lost altogether. Removal of the *L. curvispinosus* slaves causes an expansion of the repertory of the *duloticus* workers, especially with reference to brood care, but not enough to permit survival of the colony.

When two colonies of *L. curvispinosus* were placed next to each other, the larger evicted the smaller, captured its pupae, and adopted the emerging workers. The same response was shown by *L. ambiguus* colonies to those of *curvispinosus*, except that the emerging workers were killed after a few hours. The behavior is considered preadaptive to slave-making and closes all but a relatively narrow behavioral gap between free-living *Leptothorax* and *L. duloticus*.

Two forms of hostility by the slaves toward their *duloticus* mistresses are described. The *duloticus* workers also displayed aggression toward each other when deprived of both the queen and slaves. This instance of hostility among sister workers may be unique.

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