5665

Anim. Behav., 1979, 27, 202–210

RAIDING BEHAVIOUR OF TWO SPECIES OF SLAVE-MAKING ANTS, *HARPAGOXENUS AMERICANUS* (EMERY) *AND LEPTOTHORAX DULOTICUS* WESSON (HYMENOPTERA: FORMICIDAE)

BY THOMAS M. ALLOWAY

Erindale College, University of Toronto, Mississauga, Ontario, Canada

Abstract. The slave-raiding behaviour of *Harpagoxenus americanus* and *Leptothorax duloticus* is compared. In both species, raids follow 'scouting' by individuals or small groups of slave-makers. Single scouts return to their nest to lead a raiding party. Groups attack host-species nests at once, with or without recruiting additional raiders. Raiders usually guard the entrance to the raided nest, preventing workers from escaping with brood. *L. duloticus* raiders kill most adults in raided nests, but *H. americanus* raiders kill very few such individuals. *H. americanus* raiders always and *L. duloticus* raiders usually transport the raided colony's brood back to their own nest. However, *L. duloticus* colonies sometimes emigrate into raided nests.

Slavery in ants is a form of social parasitism. Slave-making (or parasite) species conduct raids against nearby colonies of other closely related slave (or host) species. During these raids, the slave-makers overwhelm the adults in slave-species colonies, capture their brood, and transport all or part of it back to the slave-makers' nest. Young slave-species workers emerging from the captured brood form a social attachment to the slave-makers and the other slaves and join in all aspects of labour in the parasite colony. Indeed the social attachment of the slaves to the slave-makers often becomes so complete that they even accompany the parasites on expeditions against other colonies of the same host species.

This paper presents a detailed comparison of the slave-raiding behaviour of two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson. A comparison of the behaviour of these species is especially interesting for several reasons. First, these slave-makers are generally considered to be rather closely related (Wesson 1937, 1939; Wilson 1971, 1975). Moreover, they enslave the same three host species (*L. ambiguus* Emery, *L. curvispinosus* Mayr, and *L. longispinosus* Roger) while coexisting sympatrically over a wide area in eastern North America. However, they show large differences in morphological specialization for their similar modes of life. *H. americanus* possesses a number of very obvious morphological modifications that seem to be adaptations for its parasitic existence (Wesson 1939; Wheeler 1910; Wilson 1971). In contrast, *L. duloticus* shows only a few quite minor anatomical peculiarities that may be specializations for slave-making (Wesson 1937; Wilson 1975). Thus, if morphological and behavioural specializations are correlated in this group of ants, we may expect that a comparison of the behaviour of these two species will throw light on the probable evolutionary history of slavery in Leptothoracine ants. However, although previous investigators (Creighton 1927, 1929; Sturtevant 1927; Talbot 1957; Wesson 1937, 1939, 1940; Wilson 1975) have studied *H. americanus* and *L. duloticus* separately, no one has previously exploited the opportunity to study their behaviour simultaneously under identical observational conditions. Thus, the full potential for comparative study has not been realized.

Materials and Methods

Colonies of *H. americanus*, *L. duloticus*, and their hosts were collected during April, May, and early June from hollow acorns and hickory nuts and from hollow milkweed stems in southern Ontario, Michigan, Illinois, and Indiana. Colonies of all species were housed in artificial nests that were designed to permit observations of behaviour inside the nest as well as outside it. The base of each nest was formed by the lid from a 10 × 30 mm plastic petri dish that had been painted green. A small hole in the side of the base served as the nest entrance. Each nest was covered with a transparent red Plexiglass lid into which a groove had been milled so that the lid snapped firmly onto the nest base. For culturing and general maintenance, nests containing colonies were placed inside larger 15 × 150-mm plastic petri dishes that provided small arenas in which the ants could forage. Colonies were offered a drop of

B

water and a drop of the artificial ant diet devised by Bhatkar & Whitcomb (1970) three times a week. While in the laboratory, colonies were maintained on a 15-h light and 9-h dark photoperiod and kept at a constant temperature of 22 C ± 1.

Slave raids were observed in square plastic arenas having an area of 2025 cm^2 and a depth of 6 cm. The sides and bottom of each arena were painted green, and each arena was covered with a tightly fitting clear plastic cover. Field data indicated that these arenas were large enough to simulate at least the minimum distances that occur between host and parasite colonies nesting in acorns in nature.

The procedure for inducing and observing slave raids consisted first of placing a nest containing a slave-maker colony, an empty nest, and a microscope slide with food and water on it in an arena at least 24 h before the commencement of observations. Immediately before beginning observations, a host-species target colony was put into the arena; and the arena was placed inside a special table designed in such a way that, with an arena in place, the top of the arena and the table top formed a level surface.

During the course of the ensuing interactions between members of the two colonies, the ants were observed either with the naked eye or with the aid of a dissecting microscope and illuminator mounted on wheels so that the whole unit could be moved easily and swiftly around on the surface formed by the lid of the arena and the table top. The microscope facilitated detailed observations of behavioural interactions and permitted the precise determination of the species of interacting ants. Microscopic determination of species was often necessary since individuals of *L. ambiguus*, *L. curvispinosus*, and *L. duloticus* cannot be reliably distinguished with the naked eye.

Observations began immediately after the target colony had been placed in the arena and continued for 6 h or until a raid had been completed. Observations were terminated and the interaction was considered to be a 'non-raid' if no slave-maker had entered the target colony within 6 h after its introduction into the arena.

A total of 30 observations of interactions between slave-maker and host-species colonies was performed during late June and July; and different colonies were used for each observation. Each of the two slave-making species was observed 15 times, each five times with each of the three host species. Thus. the study involved a 2 × 3 factorial design with an equal number of replicates in each of the six cells formed by the combinations of the two parasite and three host species.

The 30 slave-maker colonies used were selected from over 100 collected. Only relatively large, thriving colonies were employed. The reproductive female in 12 of the 15 *duloticus* and 11 of the 15 *americanus* colonies was a dealate full female. In one colony of each parasite species, the reproductive female was an ergatogyne (an individual with distinct ocelli but with a worker-like alitrunk); and in two *duloticus* and three *americanus* colonies, the apparent reproductive female was a physogastric worker. In addition to the reproductive female, the *duloticus* colonies contained means and standard deviations of 15·67 ± 8·61 *duloticus* workers, 26·27 ± 12·27 slave workers, 15·57 ± 25·75 pupae, 17·07 ± 14·51 larvae, and 7·20 ± 8·95 eggs. The *americanus* colonies contained 12·87 ± 5·83 *americanus* workers, 38·40 ± 24·99 slave workers, 9·67 ± 17·89 pupae, 13·40 ± 13·22 larvae, and 10·40 ± 7·39 eggs. Twelve *duloticus* and seven *americanus* colonies contained slaves of only one species, while three *duloticus* and eight *americanus* colonies contained two species of slaves. There were no statistically significant differences between the two parasite species in any of the demographic parameters of colonies.

All target colonies were queen-right mature colonies of their species. They contained means and standard deviations of 1·83 ± 1·46 dealate females, 30·10 ± 15·59 workers, 24·27 ± 16·62 pupae, 31·47 ± 21·05 larvae, and 22·53 ± 18·63 eggs. There were no statistically significant differences among the three species in the demographic parameters of colonies.

Results

Scouting and the Recruitment of Raiding Parties

The 30 interactions between slave-maker and host-species colonies produced a total of 23 slave raids, 13 by colonies of *H. americanus* and 10 by colonies of *L. duloticus*. In both parasite species, raids followed the occurrence of a behaviour pattern called 'scouting' (Wesson 1939, 1940). Scouting consists of slave makers emerging from their nest and wandering about in search of a host-species colony. Scouting occurred on all 23 occasions when slave raids occurred and on none of the occasions when raids did not occur. On those occasions when no raids occurred, the slave-makers simply remained

in their nests, although there was always a good deal of fighting between the slaves and the workers from the target colony. Despite this fighting, during the 6-h period allotted for a raid to begin before the target colony was removed from the arena neither the slaves nor the target-colony workers ever mounted a concerted attack on the other colony's nest.

Two forms of scouting were observed in both *H. americanus* and *L. duloticus*. Workers of the slave-making species may scout as single individuals that move completely independently of each other, or they may scout as small groups of two or more individuals that move more or less in concert and stay within 2 to 3 cm of one another. During group scouting, two or three slave-makers may be accompanied by one or more slaves. Group and individual scouting may also occur simultaneously; and individual scouts sometimes join groups that they happen to encounter, while group members sometimes stray from the group and begin scouting on their own. The mechanism by which groups of scouts maintain their cohesion is unclear. The groups seem to have no leader, and none of the group members engages in the conspicuous pheromone trail-laying or trail-following behaviours described below. Moreover, within the groups the members show a considerable amount of independent movement. For want of a better explanation, I speculate that the group members maintain visual contact with one another.

The two forms of scouting were followed by an extremely variable sequence of events once the slave-makers had discovered the target colonies. Indeed, the sequence was so variable that no two slave raids were really alike. Nevertheless, it was possible to categorize these behavioural sequences into four basic recruitment techniques.

(A) An individual scout discovers the target colony, explores it until it has discovered the colony entrance, returns to its own nest, and leads across a raiding party of slave-makers or of both slave-makers and slaves. While exploring the vicinity of the target colony, the scout may encounter target-colony workers and skirmish with them. However, lone scouts never try to enter target-colony nests. After locating the entrance to the target colony, the slave-maker quickly leaves the vicinity of the target colony and returns to its own nest via a reasonably direct route. Since the return of a successful scout invariably causes a great increase in the general activity level of the entire slave-maker colony, an increase not seen after the return of an unsuccessful scout or of a slave that has just discovered a food source, it is possible that the scout secretes a general alarm or excitement pheromone. However, no characteristic behaviour associated with the secretion of this hypothetical pheromone was observed. Then, after usually less than 1 min, the scout returns to the nest entrance, halts, extrudes its stinger while bending its gaster sharply downward so that the stinger touches the substratum, and begins to move forward out of the nest dragging its stinger along the substratum. That the scout is now very probably laying down a trail pheromone is indicated by the fact that it is immediately followed by a single file of slave-makers and sometimes slaves that adhere to the leader's path exactly while antennating the substratum more or less continuously. Trail-laying *duloticus* scouts move with a slow, halting gait strongly reminiscent of that of a *Leptothorax* host-worker leading another worker to food via a tandem run (Moglich et al. 1974). Trail-laying *americanus* scouts move faster. Finally, upon reaching the target-colony nest, the raiding party attacks it as a group. This technique was described by Wesson (1939, 1940) as being typical of both *H. americanus* and *L. duloticus*. However, in the simple form described, I have observed it in only one *duloticus* and three *americanus* raids.

(B) A group of three to six scouts discovers the target nest. Some of them begin to attack it at once, while one or two return to the home nest to recruit additional raiders. Both the scouting groups and the recruited reinforcements may consist of slaves as well as slave-makers; but a slave-maker always leads the additional raiders in a fashion identical to that of a lone scout returning to lead a raiding party. This technique was observed in six *americanus* and three *duloticus* raids.

(C) A group of scouts, which may include one or more slaves, discovers and attacks the target colony without any reinforcements being recruited until after the target colony has been defeated. This technique was observed in three *americanus* and three *duloticus* raids.

(D) A single slave-maker discovers the target colony and returns to its home nest sometimes, but not always, after discovering the entrance to the target nest. The scout excites several of its nestmates to begin group scouting. However, the scout that has discovered the target nest does not engage in trail-laying behaviour or even necessarily join the scouting group. Moreover, the scouting group seems to move more or

less at random without showing any indication of 'knowing' where the target colony is. Nevertheless, the group eventually discovers, attacks, and defeats the target colony without recruiting reinforcements. This technique was observed in one *americanus* and three *duloticus* raids.

Efforts were made to correlate demographic characteristics of slave-maker and target colonies with the use of the different techniques for recruiting raiding parties. However, owing very likely to the small number of raids observed, no significant patterns of demographic differences emerged among colonies employing the different techniques; nor were there any statistically significant differences in the use of the techniques by the two slave-making species.

Attack Strategy, Fighting Tactics, and Casualties

The next stage in a raid is the attack on the target colony, during which the raiders kill or drive away the target-colony workers and reproductives and capture as much of their brood of pupae, larvae, and eggs as possible. The attack behaviours of raiding parties of the two parasite species manifest a number of basic similarities as well as a number of fundamental differences.

In both parasite species, the slave-makers and their slaves (when present) attempt to gain entrance to the target colony as quickly as possible either by force or by somehow intimidating the target-colony workers. Once inside, the slaves (when present) attack the target-colony workers by biting and stinging them, while the majority of the slave-makers continue either to attack or to intimidate the target-colony adults. However, one or two slave-makers usually remain just inside the colony entrance and engage in what I shall call 'entrance-guarding' behaviour, a behaviour in which slaves also sometimes engage when they are present. Apparently, the function of these entrance guards is to prevent the escape of target-colony members with pieces of brood. Since the attack of a raiding party always eventually causes all uninjured target-colony workers and queens to attempt to flee with pieces of brood, the efficient functioning of these entrance guards is a crucial aspect of the attack strategy. If the entrance guards perform this task inefficiently, the target-colony workers and queens do in fact escape with a considerable portion of their brood. In the laboratory, where the target and parasite colonies were confined in an enclosed space, such escapes made little difference in the long run; the slave-makers always managed to secure all or almost all the target colony's brood eventually. However, in nature it seems likely that inefficient entrance guarding might result in the parasites' permanently losing a large portion of the target colony's brood.

The efficiency of entrance guarding varied greatly. In six *americanus* and eight *duloticus* raids, the entrance guards prevented the target-colony workers from escaping with more than three or four pieces of brood. In the other two *duloticus* raids and in five *americanus* raids, entrance guarding occurred but was less efficient, with the result that the target-colony adults escaped with up to 1/3 of their brood. Finally, in two *americanus* raids, no entrance guarding occurred during the attack by the raiders. The target-colony adults escaped with more than 1/2 their brood in one instance and with almost all of it in the other.

Since raiding parties of both parasite species enter the target nest en masse and engage in a division of labour in which some raiders attack or intimidate while others guard the target-colony entrance, the attack strategies of *H. americanus* and *L. duloticus* may be regarded as being basically similar. However, the actual fighting tactics of the two species are vastly different.

Workers in target colonies tenaciously resist the incursions of *duloticus* raiding parties, and the *duloticus* respond by biting and stinging every hostile target-colony worker and queen encountered. The result is an extremely fierce battle during which large numbers of target-colony members are stung to death. In 6 of the 10 *duloticus* raids, at least 75% of the target-colony workers in their nest at the time of the attack were killed almost immediately. In two *duloticus* raids, between 50 and 75% of the target-colony workers present were killed; and in two *duloticus* raids (the raids in which the *duloticus* manifested inefficient entrance guarding) 25 to 50% of the target-colony workers present were killed. Nevertheless, the ferocity of the *duloticus* attack seems to be finely tuned to the intensity of the resistance offered by individuals. Workers and queens attempting to leave the nest without brood and without resisting the *duloticus* are generally permitted to do so unharmed.

In contrast to the fierce resistance to *duloticus* raiders, very little resistance is offered to incursions by *americanus* raiding parties. Although target-colony workers sometimes attack and are

often attacked by the slaves that usually accompany the *americanus*, the *americanus* workers themselves are very rarely attacked. Something about the *americanus* excites almost immediate panic in the target colony. Moreover, although target-colony workers at first pick up pieces of brood and attempt to escape, an encounter with an *americanus* entrance guard is usually enough to cause a brood-laden worker to drop its burden. Even on those rare occasions when an *americanus* worker is attacked, it ordinarily manifests no resistance apart from struggling to free itself. During the course of 13 raids, no *americanus* was ever observed to bite or sting another ant.

As a result of the relative non-violence of their attacks, *americanus* raiders inflict many fewer casualties than *duloticus* raiders. Indeed, the few casualties that do occur seem to be exclusively the result of fights between slaves and target-colony workers. In 8 of the 13 *americanus* raids, all the target-colony workers in their nest at the time of the attack escaped uninjured. In three raids, there were fewer than five casualties among the target-colony workers in the nest during the attack; and in two raids there were between five and ten casualties among target-colony workers.

Wesson (1939) attributed the capacity of *americanus* workers to cause panic in target colonies to the agility and erraticness of their movements and to their tendency to nip at and 'worry' target-colony adults. However, *americanus* workers are actually less active than *duloticus* workers during attacks. Nevertheless, target-colonies fiercely resist *duloticus* attacks while panicking almost immediately upon the arrival of an *americanus* raiding party. The most likely method by means of which *americanus* workers could cause panic is by the secretion of a propaganda pheromone analogous to that employed by the Formicine slave-maker, *Formica subintegra* (Regnier & Wilson 1971). However, this interpretation cannot be accepted without reservation for *H. americanus*. A propaganda pheromone should excite both the target-colony workers and the slaves in the *Harpagoxenus* raiding party, but only the target-colony workers seem to be affected. Clearly, more work is needed before we shall understand the mechanism by means of which *americanus* incites panic in target colonies.

Brood Transport and Colony Emigration

Once the adult members of the target colony have been killed or dispersed, the final phase of the raid begins. *Americanus* raiders always transported the target colony's brood back to their nest. Usually, *duloticus* raiders did the same. However, two *duloticus* colonies emigrated into raided nests.

In both parasite species, the defeat of the target colony was always followed shortly by the recruitment of additional raiders via processions in which the slave-makers laid down pheromone trails. In all 13 *americanus* raids, some slaves were led over to the raided nest at this time; and in five *americanus* raids, only slaves were recruited. In 7 of the 10 *duloticus* raids, the recruits included both slave-makers and slaves. However, in three raids (including the two in which the *duloticus* emigrated into the raided nest), only additional slave-makers were recruited.

In all the *americanus* raids and in the seven *duloticus* raids during which slaves as well as slave-makers were recruited, the augmented raiding party somehow divided into three contingents of brood carriers, entrance guards, and 'auxiliaries'. In both parasite species, the brood-carrying contingent ordinarily consisted of no more than five or six and usually of only two or three slave-makers. These workers made repeated trips between the raided nest and the slave-makers' home nest until all or almost all the captured brood had been transported. Only a few eggs or very small larvae were occasionally left in the raided nest or dropped just outside it. Slaves also, albeit rarely, carried captured brood. However, slaves moved more slowly than the slave-makers, did not carry the brood over as direct a route, and usually transported only one and never more than three pieces of brood.

The second contingent consisted of entrance guards in the raided nest. These guards fended off any attempts by members of the target colony to recover pieces of their brood. During *duloticus* raids, the guard contingent usually consisted of one or two slave-makers and one or two slaves, although it sometimes consisted of slave-makers or slaves only. During *americanus* raids, the guard contingent usually consisted of slaves only, although an *americanus* sometimes joined the guard contingent briefly.

The third contingent consisted of 'auxiliaries', slave-makers or slaves or both, that remained inside the raided nest (usually in the vicinity of the brood pile) without appearing to do much

of anything. The auxiliary and guard contingents frequently exchanged members. However, it was rare for a brood carrier to become a member of one of the other contingents or *vice versa*.

Shortly before or after the last piece of brood had been transported, the slave-makers and their slaves began to leave the raided nest. The nest was usually deserted entirely within about an hour after the last piece of brood had been transported.

As noted above, two *duloticus* raids were unusual in that the parasite colony moved into the raided nest instead of transporting the captured brood back to their home nest. Moreover, during one other raid, the behaviour of the raiders suggested that an emigration almost occurred. During these three raids, after the target colony had been defeated, the raiders began the usual recruitment of additional nestmates. However, instead of recruiting a combination of slave-makers and slaves, only slave-makers were led to the raided nest. Moreover, the recruitment continued until all the *duloticus* workers had assembled in the raided nest on two occasions and until all except one of them had assembled there on the third. This assemblage of slave-makers then set about removing the dead bodies of the target-colony adults from the raided nest and examining the captured brood in an unusually detailed way with their mandibles and antennae. On the first occasion when this behaviour occurred and was followed by an emigration, I failed to realize at first the significance of what was happening and did not note how long the period of brood examination lasted. However, on the second occasion when an emigration also occurred and on the third occasion when no emigration occurred, the periods of brood examination lasted 87 and 108 min respectively.

On the third occasion, when the period of examination behaviour was followed by the transport of the captured brood back to the home nest, the assembled slave-makers split into the usual three contingents. Brood transport then proceeded in the normal way except that no slaves were present in the guard and auxiliary contingents. On the other two occasions when emigrations did occur, the assemblage of slave-makers divided into guard and transport contingents, but there were no 'idle' auxiliaries among the *duloticus* until the emigration was well under way. On these occasions, instead of removing the captured brood from the raided nest, the carriers began to return to their old nest, pick up pieces of their own brood, and try to make their way to the nest entrance. Whenever a carrier managed to get a piece of the *duloticus* brood out of the old nest, it carried it to the raided nest. However, the activities of the carriers greatly excited their slaves. Although the slaves did not seem hostile to the *duloticus*, they formed a kind of milling 'mob' inside the nest entrance that made it mechanically difficult for a *duloticus* worker to get to the nest entrance with a piece of brood. Whenever a *duloticus* was seriously impeded in its progress, it would put down the piece of brood that it had been carrying, make its way through the crowd of slaves to the nest entrance, and pick up and carry a slave across to the raided nest. As the number of slaves in the old nest was thus reduced, brood transport became more rapid. During this period, the *duloticus* queen was carried over. Finally, in the late stages of both emigrations, a few slaves began returning to the old nest and carrying other slaves to the raided nest. On both occasions, the emigration into the raided nest was completed within about 90 min after the carriers began transporting brood and slaves.

Fate of the Captured Brood

Following raids, workers of both parasite species and their slaves were observed eating large numbers of captured eggs and small larvae. However, the fate of captured queen and male pupae was quite different in *duloticus* and *americanus* nests. *Duloticus* colonies always ate all host-species sexual pupae that they captured. Some captured sexual pupae were also eaten by *americanus* colonies. However, many captured sexual pupae were permitted to mature in *americanus* nests; and host-species alates emerging from them were permitted to leave the *americanus* nests without being molested in any way.

This difference between *duloticus* and *americanus* colonies is probably not just a laboratory artifact. Colonies of *americanus* collected when winged reproductives are present in host-species colonies also frequently contain host-species alates. However, I have never collected a *duloticus* colony containing an adult host-species reproductive. These combined field and laboratory data lead me to hypothesize that *americanus* colonies regularly rear host-species reproductives and permit them to leave their nests to go out on nuptual flights. In contrast, *duloticus* colonies seem to use host-species reproductive pupae as a supplementary food source.

Behaviour of Target Colonies and Miscellaneous Observations

Workers from target colonies frequently encountered foraging slaves and scouting slave-makers. Encounters with both the slaves and the slave-makers were invariably hostile.

Numerous fights between the slaves and the target-colony workers always occurred in the arena before the slave-makers discovered and attacked the target colony. Such fights also characterized those interactions that did not culminate in slave raids. During these fights, the slaves and target-colony workers bit and stung one another, and numerous casualties on both sides resulted.

Whenever scouts of the slave-maker species were encountered, they were also attacked by the target-colony workers. The results of these encounters were quite different for *duloticus* and *americanus* scouts. *Duloticus* scouts regularly stung attacking target-colony workers to death. However, *americanus* scouts did not fight back actively. Nevertheless, most *americanus* scouts managed to escape from their attackers by somehow confusing them. In a typical encounter, an *americanus* would be discovered near the nest entrance by several target-colony workers. While two or three workers seized the intruder, the rest returned to the nest and excited their nestmates, possibly by emitting an alarm pheromone. As a result, numerous agitated workers would emerge from the target colony. However, new target-colony workers arriving on the scene of the fight with the *americanus* would usually attack their nestmates that were fighting with the intruder, instead of the *americanus* itself; and the *americanus* would escape. Often the resultant fighting among target-colony workers became quite widespread and produced casualties so that the target colony was already somewhat weakened and 'demoralized' when the *americanus* raiding party arrived.

An empty nest was always placed in the arena to determine whether survivors from target colonies would move back into their old nests or into the new nests after raids. Target-colony survivors never tried to reoccupy their old nest and usually tried to move into the new nest. However, their attempts to do so were always short-lived. If the survivors had escaped with a significant portion of their brood, their new home was always raided by the slave-makers. If little or no brood had been retained, the slave-makers often ignored them. However, the remnant was continually harassed by slaves until it had been dispersed and the survivors had been killed one by one.

Nevertheless, much of this post-raid harassment was probably produced by the unnatural confinement of the target-colony remnant in close proximity to the parasites' nest. In nature, it seems likely that remnants would stand a much better chance of long-term survival, particularly following the relatively non-violent raids of *H. americanus*.

Discussion

Wesson (1940) noted that, whereas *duloticus* raiders rely mainly on brute force to subdue target colonies, *americanus* raiders excite target colony members to flee. The results of the present study strongly confirm and extend Wesson's observation. In addition, when viewed in the light of subsequent information regarding territorial behaviour in *L. ambiguus* and *L. curvispinosus*, the present results decidedly clarify the probable evolutionary history of slavery in Leptothoracine ants.

Wilson (1975) observed the behaviour of large colonies of *L. curvispinosus* that had been placed in arenas with smaller colonies of their own species. Under these circumstances, the workers from the large colony attacked and killed those from the smaller colony and carried off the small colony's brood to the large colony's nest. Workers emerging from captured worker pupae were adopted by the large colony. In a parallel series of experiments, large colonies of *L. ambiguus* were placed near small *curvispinosus* colonies. In two of four instances, the two colonies co-existed. In the other two instances, the *ambiguus* attacked, killed the *curvispinosus*, and stole their brood. However, alien *curvispinosus* emerging in the *ambiguus* nests were killed.

As Wilson (1975) noted, these results strongly implicate territory-defence behaviour as an evolutionary preadaptation to slave-raiding in Leptothoracine ants. All that would be required to transform non-parasitic species such as *L. ambiguus* or *L. curvispinosus* into facultative slave-makers would be a slightly enhanced tendency to tolerate the presence of workers of a closely related species as nestmates.

The results of the present study may be interpreted as indicating that the raiding behaviour of *L. duloticus* is still quite primitive in the sense that it still resembles intercolonial territorial battles in two crucial respects. Large numbers of adults from target colonies are killed; and

the target colonies' sexual pupae, small larvae, and eggs are eaten. While such destructive behaviour is clearly adaptive for a free-living species dealing with territorial competitors, it seems likely to lead to periodic shortages of host-species colonies in the vicinity of *duloticus* nests. Viewed in this light, it is probable that the tendency of *duloticus* colonies to emigrate into raided nests may be either a response to such shortages or an adaptation for their avoidance.

In this context, the raiding behaviour of *H. americanus* appears to be relatively advanced in comparison to that of *L. duloticus*. When encountered as scouts, *americanus* workers remain passive instead of attacking the target colony workers. However, probably by secreting a contaminating pheromone that causes other target-colony workers to mistake a nestmate that has been attacking an *americanus* scout for a member of another colony, the *americanus* scouts cause fighting to break out among the target-colony workers. The resulting confusion usually permits *americanus* scouts to escape while simultaneously weakening the social cohesion of the target colony even before the *americanus* raiders arrive. When the raiders do arrive, they cause the target colony to panic. Most of the target-colony adults and queens flee unharmed, leaving the *americanus* and their slaves in possession of the brood. Finally, the *americanus* capture and rear much of the target colony's sexual brood and permit emerging host-species reproductives to leave their nest unharmed. This rearing of host-species sexual pupae is an especially interesting behavioural adaptation for a social parasite, since it involves the failure to exploit an immediately available food source. Since the uninjured queens and relatively intact worker force of a target colony are probably often capable of rearing new broods for the *americanus* to raid in subsequent years and since young host-species queens probably mate and found new host-species colonies near the *americanus* nests from which they emerge, the overall *americanus* raiding strategy appears to be a much more efficient means of husbanding host-species resources than the destructive strategy of *L. duloticus*. Perhaps for this reason, *americanus* colonies are on the average two to three times as abundant as *duloticus* colonies in many regions of eastern North America where the two parasites occur sympatrically (personal observations).

However, despite these important differences in the raiding behaviour of *H. americanus* and *L. duloticus*, the present study confirms and extends our understanding of numerous other ways in which the behaviour of these two species is closely similar. The occurrence of group scouting and entrance guarding in both species and the fact that both species employ a similar diversity of techniques in raider recruitment and an identical division of labour during brood transport are examples of behavioural similarities described here for the first time. However, in the light of data indicating that the European slave-maker *Harpagoxenus sublaevis* recruits raiding parties via tandem running (Buschinger & Winter 1977), perhaps the most interesting similarity between primitive *L. duloticus* and advanced *H. americanus* is the fact that successful scouts of both species recruit raiding parties by laying down pheromone trails for their nestmates to follow.

Recruitment to food sources via tandem running is a very widespread and perhaps nearly universal phenomenon in the genus *Leptothorax* (Moglich et al. 1974), and Wilson (1971) has argued that tandem running is an evolutionary precursor to pheromone trail-laying in ants. Thus, the use of tandem running is an evolutionary primitive trait in *H. sublaevis*. For this reason, the occurrence of processions in morphologically even more primitive *L. duloticus* is somewhat surprising. If traditional views about the separate evolutionary origins of *H. americanus* and *L. duloticus* are accepted (Wesson 1940; Wilson 1975), the recruitment of raiders by processions in these two species is an extremely interesting example of the convergent evolution of behaviour.

Acknowledgments

This research was supported by Grant No. A0301 from the National Research Council of Canada. I wish to thank Mr Franz Schmidt and Mr Brian Johnston for their assistance in data collection and Professor Rona Abramovitch, Professor Kirk Blankstein, Professor Alfred Buschinger, Professor David Gibo, Dr Mary Talbot, Mr James Beckwith, and Mr Robin Stuart for their comments on the manuscript.

REFERENCES

Bhatkar, A. & Whitcomb, W. H. 1970. Artificial diet for rearing various species of ants. *Fla. Entomologist*, 53, 217–232.

Buschinger, A. & Winter, U. 1977. Rekrutierung von Nestgenossen mittels Tandemlaufen bei Sklavenraubzügen der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.). *Ins. Soc.* (Paris), 24, 183–190.

Creighton, W. S. 1927. The slave raids of *Harpagoxenus americanus*. *Psyche*, **34**, 11–29.

Creighton, W. S. 1929. Further notes on the habits of *Harpagoxenus americanus*. *Psyche*, **36**, 48–50.

Moglich, M., Maschwitz, U. & Holldobler, B. 1974. Tandem calling: a new kind of signal in ant communication. *Science, N.Y.*, **186**, 1046–1047.

Regnier, F. E. & Wilson, E. O. 1971. Chemical communication and 'propaganda' in slave-maker ants. *Science, N.Y.*, **172**, 267–269.

Sturtevant, A. H. 1927. The social parasitism of the ant, *Harpagoxenus americanus*. *Psyche*, **34**, 1–9.

Talbot, M. 1957. Population studies of the slave-making ant *Leptothorax duloticus* and its slave *Leptothorax curvispinosus*. *Ecology*, **38**, 449–456.

Wesson, L. G., Jr. 1937. A slave-making *Leptothorax* (Hymen.: Formicidae). *Entomol. News*, **48**, 125–129.

Wesson, L. G., Jr. 1939. Contribution to the natural history of *Harpagoxenus americanus* (Hymenoptera: Formicidae). *Trans. Am. Entomol. Soc.*, **65**, 97–122.

Wesson, L. G., Jr. 1940. Observations of *Leptothorax duloticus*. *Bull. Brooklyn Entomol. Soc.*, **35**, 73–83.

Wheeler, W. M. 1910. *Ants: Their Structure, Development, and Behavior*. New York: Columbia University Press.

Wilson, E. O. 1971. *The Insect Societies*. Cambridge, Mass.: Belknap Press of Harvard Unversity Press.

Wilson, E. O. 1975. *Leptothorax duloticus* and the beginnings of slavery in ants. *Evolution*, **29**, 108–119.

(*Received* 7 *October* 1977; *revised* 17 *May* 1978; *MS. number:* A2102)