

POLYDOMY IN THE SLAVE-MAKING ANT,
HARPAGOXENUS AMERICANUS (EMERY)
(HYMENOPTERA: FORMICIDAE)¹

BY

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INTRODUCTION

Slavery in ants is a form of social parasitism in which parasitic "slave-making" species exploit the labor of workers derived from host-species colonies. The slave makers raid host-species nests, where they capture all or part of the brood. Subsequently, workers maturing from the captured brood form a social attachment to the slave makers and perform all the usual worker-ant functions in the parasites' colony (see review in Buschinger *et al.* 1980).

Harpagoxenus americanus (Emery) is an obligatory slave maker living in eastern North America, where it forms mixed colonies with members of certain *Leptothorax* species (see Alloway 1979). Two kinds of *H. americanus* nests are found: "primary nests" containing a single slave-maker queen and slaves with or without slave-maker workers, and "secondary nests" consisting of slave-maker workers and slaves without a slave-maker queen (Creighton 1927; Sturtevant 1927; Buschinger & Alloway 1977). Primary nests are apparently established when a parasite queen successfully invades a host-species nest (Wesson 1939), but the origin of secondary nests is questionable. The problem is compounded by the fact that secondary nests are usually more numerous than primary nests and frequently produce slave-maker females (workers and/or queens) from

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their broods (Wesson 1939; Buschinger & Alloway, 1977). In the related European slave maker, *H. sublaevis*, "ergatoid queens" (individuals with fully functional ovaries and a spermatheca, but with a more or less worker-like external morphology) are common and function as the usual female reproductives (Buschinger, 1978). However, Buschinger and Alloway (1977) found that, while many *H. americanus* workers have functional ovaries and lay eggs that can mature to produce males, they rarely, if ever, possess a spermatheca. Thus, "ergatoid queens" are absent or very rare in *H. americanus*. Moreover, these authors thought that thelytoky was unlikely in this species.

Wesson (1939) observed the formation of secondary nests in the laboratory. Slave-maker colonies which had conducted several ordinary slave raids sometimes concluded the final raid of the season by splitting into two components. In these cases, a few slave-maker workers and slaves remained indefinitely in the raided nest with part of the captured brood. Wesson suggested that this might be a sufficiently common late-season activity to account for the frequent occurrence of secondary nests. However, even if secondary nests are formed in this manner, there are still two possibilities for the relationship between secondary and primary nests and for the origin of the female slave-maker brood in secondary nests. Following their formation, secondary nests might become autonomous entities functionally separate from their parental primary nests. In this case, if we exclude thelytoky, the female slave-maker brood in secondary nests would have to be derived exclusively from brood carried over from the primary nest when the secondary nest was initially occupied (Buschinger & Alloway 1977). Alternatively, the primary nest and one or more secondary nests might comprise a single multiple-nest (polydomus) colony (Sturtevant 1927). Interactions between the nests of such polydomous colonies would be protracted, and the slave-maker queen would continue to supply female brood for all nests in her colony. The latter possibility is supported by the fact that polydomy of this type has recently been demonstrated in two of the host species of *H. americanus*, *Leptothorax ambiguus* Emery and *L. longispinosus* Roger (Alloway *et al.* 1982). The objective of the present study was to examine these two possibilities by collecting and mapping *H. americanus* and host-species nests in nature, reconstructing their spatial relationships in the laboratory, and observing the interactions among them.

MATERIAL AND METHODS

The ants were collected on the Erindale Campus of the University of Toronto in Mississauga, Ontario, during the spring and summer of 1980 and 1981. Since our purpose was to determine whether colonies of *H. americanus* sometimes occupy more than one nest, we looked for areas where two *H. americanus* nests occurred within 2 m of each other. Whenever such a place was located, we layed out a 2 m by 2 m quadrant centering on the two nests and then collected, numbered and mapped the location of every *H. americanus* nest and every nest of its host species (*L. ambiguus* and *L. longispinosus*) in the quadrant. In some cases, adjacent quadrants were combined to permit the collection of a larger group of slave-maker nests.

In the laboratory, we removed the ants and their brood from their natural nests and established them in artificial nests of the type described by Alloway (1979). For censusing, the artificial nests were placed in petri dishes (diameter = 14.5 cm; height = 1.5 cm) containing a water bottle and food (Bhatkar & Whitcomb 1970). Then the ants were transported to an unairconditioned, naturally lighted room. On the floor of this room, quadrants were layed out with masking tape; and the field maps were used to locate the position occupied by each nest. A thick layer of petroleum jelly on the masking tape formed a barrier which confined the ants to their respective quadrants. A water bottle and food were placed near each nest. In this way, it was possible to set up the artificial nests so that we duplicated the spatial arrangement of the natural nests.

In addition to the quadrants collected from the field, we set up one control quadrant to study behavioral interactions between two *H. americanus* nests which had not been collected near one another in nature. The sides of this control quadrant were 100 cm long, and the two nests were placed 80 cm apart.

During the course of our observations, some of the ants were marked so that they could be individually identified. Each mark consisted of a very small dot of colored nail polish applied to the dorsal surface of the gaster with the tip of a minuten pin embedded in the end of a wooden stick. Ants remained marked for periods of 1 day to 1 month.

Observations were made 8 h a day, 5 days a week between 10 June and 27 August 1980 and between 7 May and 30 August 1981. Five quadrants were collected and observed during 1980; and 14 quadrants were collected and observed during 1981.

RESULTS

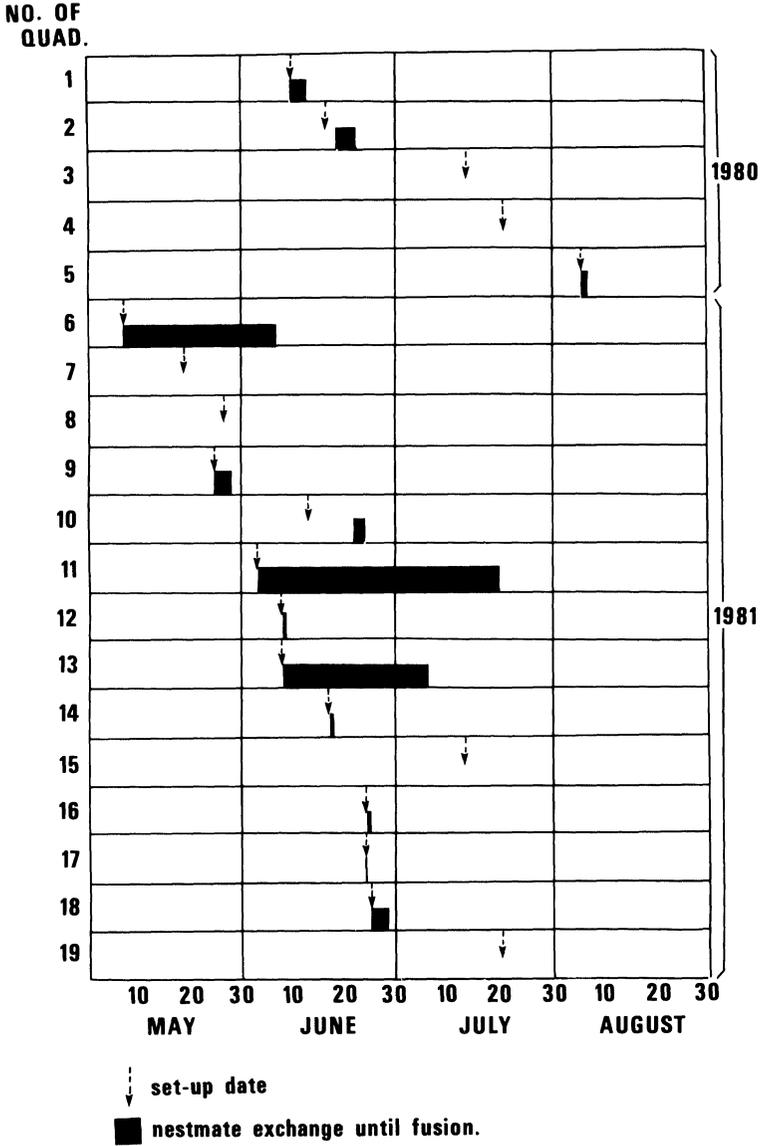
There was a total of 19 quadrants. However, quadrant 1 was merged with quadrant 2 and quadrant 9 with quadrant 10 when an additional *H. americanus* nest was found in close proximity to a group of other *H. americanus* nests, but outside the original quadrant boundary. Altogether, the quadrants contained 49 *H. americanus* nests, 57 *L. ambiguus* nests, and 59 *L. longispinosus* nests (see Table 1).

Our most common observation was "fusion" of all the *H. americanus* nests in a quadrant. By "fusion", we mean that eventually all the ants from two or more *H. americanus* nests peacefully moved into a single nest after exchanging adult nest-mates and brood among the different nests for varying lengths of time (Figure 1). This exchange was carried out exclusively by slaves. The ability of nests to fuse shows that there is no behavioral barrier to interactions and exchange of nestmates among nests and thus indicates either that all the ants are members of the same polydomous colony or that *H. americanus* is a unicolonial species with no behavioral barriers between its nests. Fusion of all the slave-maker nests was observed in quadrants (1 + 2), 5, 6, (9 + 10), 11, 12, 13, 16, 17, and 18, in which there was never more than one slave-maker queen.

However, we did not always observe fusion among *H. americanus* nests:

- a. In the control quadrant where two *H. americanus* nests from different collection sites were arbitrarily set up near each other, the ants showed no tendency to fuse; and the slave makers from one nest successfully raided the other slave-maker nest.
- b. Quadrants 3 and 8 each contained two *H. americanus* queens living in different nests with slaves and a brood. In quadrant 3, there was little behavioral interaction between the ants in the two nests. However, in quadrant 8, after the brood matured, the *H. americanus* workers in one nest raided the other slave-maker nest.
- c. In quadrant 4, there was little contact between the ants in the two *H. americanus* nests, but the small amount of contact observed was hostile.
- d. In quadrant 14, slaves and slave makers in two nests fused and then fought with the slaves and slave makers in a third nest.

Figure 1 - Set-up date, duration of nestmate exchange until date of fusion.



e. In quadrant 19, both the slaves and the slave makers from different nests fought whenever they met; and the slave makers in one nest mounted an incomplete raid against the other slave-maker nest.

These observations indicate that *H. americanus* is not a unicolonial species. Aggressive behavioral barriers preventing the exchange of nestmates and nest fusion exist between some *H. americanus* nests. This fact strengthens the conclusion that exchange of nestmates and brood and nest fusion, when they do occur, are indicative of the existence of a polydomous colony.

Somewhat peculiar partial fusions were observed in quadrants 7 and 15. In both quadrants, the slaves peacefully moved into a single nest. In quadrant 7, the slave makers from the two nests fought. In quadrant 15 where there were 5 *H. americanus* nests, some of the slaves attacked slave makers which had been living in other nests prior to the fusion. These partial fusions may represent situations in which lack of contact between nests had begun to produce autonomy between nests.

Once the raiding season was over, we observed the formation of secondary nests in quadrants 1 and 6. In both quadrants, some of the ants which had been occupying a single nest moved into a second nest. In both cases, exchange of nestmates and brood continued for two weeks, when observations ended.

In 7 quadrants, we were unable to find an *H. americanus* queen, despite our efforts to collect each nest completely and to search beyond quadrant boundaries for additional slave-maker nests belonging to these nest groups (see Table 1). However, in each of these cases, all the maturing *H. americanus* adults were males, a fact which indicates that these particular nests had not been receiving female brood from a primary nest and is consistent with the supposition (Buschinger & Alloway 1977) that thelytoky does not occur in *H. americanus*.

The total number of adults of various species in all nests studied is summarized in Table 1. The total number of *H. americanus* workers was 115, with the average slave-maker nest containing about 2 *H. americanus* workers. The largest number of slave makers in a single nest at the time of the original census was 13; and the largest number of nests in a single apparently polydomous *H. americanus* colony was 6 in quadrant (9 + 10). Altogether, this colony contained 19 *H.*

americanus workers, 54 *L. longispinosus* slaves and 53 *L. ambiguus* slaves. The average distance between *H. americanus* nests in nest groups apparently comprising a single colony was 43.5 cm, with a range of 11 to 159 cm. The average distance between *H. americanus* nests among which there were aggressive interactions was 61.36 cm, with a range of 19 to 180 cm.

In the *H. americanus* nests, *L. longispinosus* slaves outnumbered *L. ambiguus* slaves by a ratio of almost 4:1, the total number of slaves being 803 (79.5%) for *L. longispinosus* and 207 (20.5%) for *L. ambiguus*. All the *H. americanus* colonies contained *L. longispinosus* slaves, and 9 colonies contained slaves of both species. However, none of the *H. americanus* colonies used in this study had only *L. ambiguus* slaves, although such colonies are occasionally found in the Toronto region (Alloway unpublished data). Nevertheless, 7 of the quadrants studied contained no nests of free-living *L. longispinosus*, and one of the quadrants in which there were *L. ambiguus* slaves contained no nests of free-living *L. ambiguus* (see Table 1). Unenslaved nests of *L. longispinosus* were on average somewhat more populous than the unenslaved nests of *L. ambiguus*, the mean number of workers per nest being 25.6 for *L. longispinosus* and 16.8 for *L. ambiguus*.

DISCUSSION

Our observations indicate that many *Harpagoxenus americanus* colonies are polydomous. This conclusion is based primarily on observations of peaceful interactions and of nest fusion among nests collected close together in nature, contrasted with observations that ants from different *H. americanus* nests do not always interact peacefully. The fighting and raiding observed indicate that *H. americanus* does not possess a unicolonial population structure. Thus, peaceful exchange of nestmates and nest fusions, when they occur, signify the existence of polydomous colonies. However, polydomy in *H. americanus* is not obligatory. New colonies are monodomous, becoming polydomous as they grow. Finally, our observations of partial fusions suggest that nests in polydomous colonies may gradually become autonomous, perhaps due to cessation of regular contact between nests. Under these circumstances, new queenless "secondary colonies," similar to those envisaged by Wesson (1939), could be formed.

Table 1. Total number of nests and individuals by species in each quadrant.

Quad No	H a		slaves				nests	free living						total of all nests
	♀	♂	l	l	l	a		L 1		L a		L a nests		
								♀	♂	♀	♂			
1	1	5	0	44	0	13	2	0	0	2	70	4	6	
2	1	8	0	44	0	23	3	1	53	3	112	7	11	
3	2	0	0	24	0	0	2	2	63	3	0	0	5	
4	1	6	0	22	0	0	2	4	112	5	0	0	7	
5	0	6	0	21	0	0	2	2	116	3	0	0	5	
6	1	11	0	131	0	0	3	2	166	5	2	99	10	
7	0	8	0	67	0	0	2	7	291	13	0	0	15	
8	2	2	0	39	0	0	2	4	125	6	0	0	8	
9	0	7	0	37	0	10	6	0	4	2	9	107	15	
10	0	19	0	54	0	53	2	1	82	3	19	261	19	

11	0	11	0	64	0	3	3	1	76	4	8	136	7	14
12	0	3	0	21	0	0	2	5	204	7	4	29	2	11
13	0	6	0	37	0	63	3	0	0	0	2	18	3	6
14	0	4	0	15	0	5	3	0	0	0	4	100	7	10
15	0	4	0	22	1	42	5	0	0	0	8	57	5	10
16	1	5	0	52	0	0	3	0	0	0	0	0	0	3
17	1	14	0	84	0	18	3	0	0	0	0	0	0	3
18	1	7	0	36	0	0	2	0	0	0	0	0	0	2
19	1	1	0	70	0	0	2	1	222	8	0	0	0	10
TOT	11	115	0	803	1	207	49	30	1509	59	59	958	57	164

H a = *Harpagoxenus americanus*.

L 1 = *Leptothorax longispinosus*.

♀ = queen. ♂ = worker.

L a = *Leptothorax ambiguus*.

Nevertheless, the fact that ants which had been living in several different nests in nature so frequently moved into a single artificial nest in the laboratory is somewhat problematic. Under our laboratory conditions, polydomy seldom persisted, possibly because our artificial nests were somewhat more spacious than the acorn nests which these ants inhabit in nature. If the ants live in more than one acorn because no single acorn is large enough for the whole colony, then giving the colony a larger artificial nest might produce nest fusion. However, many factors other than space may be involved in producing and maintaining polydomy in these ants (see discussion in Del Rio Pesado, 1983).

Our observations of nest divisions in two quadrants further supports the polydomy hypothesis. However, the nest fusions which we saw did not closely resemble those described by Wesson (1939). In only one of our colonies did raiding parties tend to remain in target nests; and even these raiders returned home after 1 to 3 days. What we observed was that ants which had been occupying one nest came to occupy two nests after the "raiding season" was over.

Several previous investigators have noted that many *H. americanus* nests are queenless (Buschinger & Alloway 1977; Creighton 1927; Sturtevant 1927; Wesson 1939). The usual conjecture has been that most of these queenless nests are "branches" located near queenright nests. Our data confirm this supposition by showing that many queenless nests are parts of queenright polydomous colonies. However, there were 7 quadrants in which we could not find a nest containing an *H. americanus* queen. Since these queenless nests produced only male slave-maker brood, it is unlikely that they represent components of a queen-right polydomous colony; and the males produced in these nests are probably the offspring of *H. americanus* workers (Buschinger and Alloway 1977). Some of these isolated nests may be remnants of colonies whose queen has died, while others may be products of long-distance raids from which the raiders failed to return. The presence in some *H. americanus* nests of slaves belonging to a species for which there were no free-living nests in the same quadrant suggests that *H. americanus* raids may occur over distances of several meters; and far-ranging raiders may sometimes fail to return to their base (Creighton 1927).

In our study area, *L. longispinosus* slaves outnumbered *L. ambiguus* slaves by a ratio of almost 4:1. This finding is typical throughout southern Ontario and the adjacent parts of New York state,

despite the fact that *L. ambiguus* colonies are generally more abundant than *L. longispinosus* colonies (Alloway *et al.* 1982). Two factors probably account for the prevalence of *L. longispinosus* slaves in *H. americanus* nests. First, *H. americanus* seems to manifest an ecological preference for rather cool, shady places, a habitat preference which closely matches that of *L. longispinosus*. Second, at our study site, we found that *L. longispinosus* nests were on average more populous than *L. ambiguus* nests. Thus, a raid against a nest of *L. longispinosus* might net more worker pupae than a raid against a nest of *L. ambiguus*.

SUMMARY

Field maps were made while collecting nests of the slave-making ant, *Harpagoxenus americanus*, and two of its host species, *Leptothorax ambiguus* and *L. longispinosus*. The ants were then transferred to artificial nests arranged to reconstruct the natural spatial relationships among nests. Ants from adjacent slave-maker nests often exchanged nestmates and brood for a period of time before moving into a single nest; and ants which had been living in a single nest in the laboratory sometimes moved into two nests. However, in other instances, ants from adjacent nests fought. These observations were interpreted as indicating that colonies of *H. americanus* sometimes occupy more than one nest (facultative polydomy). Nest population data were also presented and discussed.

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