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Dominance Hierarchies in *Leptothorax* Ants

Abstract. *The social organization of* Leptothorax allardycei *is unique among ant species thus far studied. The workers form linear dominance hierarchies characterized by routine displays of dominance, avoidance behavior, and even fighting. The high-ranking ants are favored in liquid food exchange, have greater ovarian development, and produce 20 percent of the eggs.*

The typical social system of ant species is based on a strict division of labor: the queen is specialized for reproduction and the workers gather food, rear progeny, and defend the colony (*1*, *2*). My research on *Leptothorax* (= *Macromischa*) *allardycei* has revealed that the social behavior of this neotropical myrmicine differs from that of all other known species of ants. Reproductive competition among the workers is resolved through the formation of a dominance hierarchy involving routine displays of dominance, avoidance behavior, and even fighting.

An agonistic encounter between two workers of *L. allardycei* begins with the dominant ant touching the submissive ant with its antennae (*3*). There is brief pause before the dominant either rapidly turns or lunges toward the subordinate (Fig. 1). It then pummels the gaster, thorax, or head of the subordinate with its mandibles. The encounter may continue, with the dominant ant advancing onto the top of the subordinate, sometimes climbing clear of the nest floor and standing on the subordinate. The typical response of the subordinate is to crouch and freeze, with the antennae drawn back to the sides of the head. It stays in this position until the dominant moves away.

Newly eclosed adults do not always conform to the above generalizations, and sometimes their responses result in fights. The intensity of these encounters can cause the combatants to fall and struggle on the nest floor. However, injuries have not been observed as a result of these encounters. *Leptothorax allardycei* workers possess a well-developed sting but do not use it in dominance encounters.

The ants also exhibit avoidance behavior. In my examination of this phenomenon, a behavioral sequence was labeled avoidance only if an individual stopped abruptly while moving through the nest, directed its antennae toward a particular ant, and then darted away in the direction from which it came. In each such instance a lower ranking worker was avoiding a higher ranking worker ($P < .001$, modified binomial test; $N = 24$).

Tables 1 and 2 show examples of dominance hierarchies in two colonies of *L. allardycei*. In general the hierarchies are almost perfectly linear. Less than 0.5 percent of the interactions are reversals. The only change in rank results from the assimilation of newly eclosed workers into the hierarchy (*4*). Dominance activity parallels rank (*5*). The highest ranking worker accounted for 43 percent of all displays of dominance and the second ranking worker accounted for 28 percent.

High-ranking workers gain a twofold advantage from their domination of coworkers: they receive more liquid food from nest mates and they gain a reproductive advantage by laying male-producing eggs.

It is typical for liquid food to be mutually exchanged among workers of social insect colonies (*6*). However, in *L. allardycei* food transfer is unidirectional; high-ranking workers receive food from low-ranking workers but do not reciprocate (*7*). From observations of liquid food transfer between workers of known rank, I calculated that the probability that rank is not associated with direction of food transfer is .0012 (Kendall's rank correlation). While this trophic advantage is an important feature of the social structure, there is no fitness advantage to the worker unless it is translated into egg laying.

A fitness advantage to unfertilized,

Table 1. Dominance hierarchy constructed from observation of 200 interactions in a queenright colony over 18.2 hours. Each entry is the number of times an interaction occurred between the ants indicated.

Dominant ants	Subordinate ants																Total
	oe	he	po	sa	lo	mi	lp	pa	da	ch	fa	do	li	bl	le	ri	
oe	–	43	19	18	1	2	2			1				1	1	2	90
he		–	45	20	3	1	5			1		1	1			1	78
po			–	3	1	5	3	2		1							15
sa				–	2	3	2	1		2	1						11
lo					–	1											1
mi						–	2			1			1				4
lp							–										
pa								–									
da									–							1	1
ch										–							
fa											–						
do												–					
li													–				
bl														–			
le															–		
ri																–	

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high-ranking workers can be expressed only through the production of males. Because of the haplodiploid sex-determining system, unfertilized eggs produce males and fertilized eggs produce females (*8*). If reproduction is restricted to high-ranking workers, ovarian development should be greatest in the highest ranking workers. The probability that ovarian development is not associated with rank is .024 (Kendall's rank correlation).

Dissection showed that the high-ranking workers do have substantially greater ovarian development (*9*). To ascertain whether they make a significant reproductive contribution to the colony, the ovaries of the living workers were stained with Sudan Black while the queen was left unstained (*10*). Thus eggs laid by the workers were blue and eggs laid by the queen were white. The percentage of worker-laid eggs in the colony was 21.8 (*11*). These eggs underwent apparently normal development and produced males.

Thus the division of reproductive effort is considerably more complicated in *Leptothorax allardycei* than in other species of ants. It can be argued that there are two reproductive castes: the queen, who is responsible for production of all the females, and the high-ranking workers, who account for at least a significant proportion of male production. Aggressive competition among the workers is resolved through the formation of a dominance hierarchy in which dominant ants enjoy both nutritive and reproductive benefits.

The evolutionary significance of this social organization is that it has characteristics intermediate between those of the supposed nonsocial ancestors of ants and those of advanced eusocial species. Consideration of the social organization of this species must alter the conception of the reproductive options available to the worker caste of social insects.

Table 2. Dominance hierarchy constructed from observation of 361 interactions in a queenless colony over 14.8 hours. Interactions are 2.2 times as frequent in the queenless colony as in the queenright colony.

Dominant ants	Subordinate ants												Total
	ca	me	st	po	cI	cII	sq	ta	u	ro	an	ni	sl	
ca	–	34	53	33	14	9		1				1		145
me		–	31	22	7			1	1					62
st			–	23	17	20			1		1			62
po				–	36	27	1					1		65
cI					–	6	1		3	1	1	1		13
cII						–	3	3	3	3		1	1	14
sq							–							
ta								–						
u									–					
ro										–				
an											–			
ni												–		
sl													–	

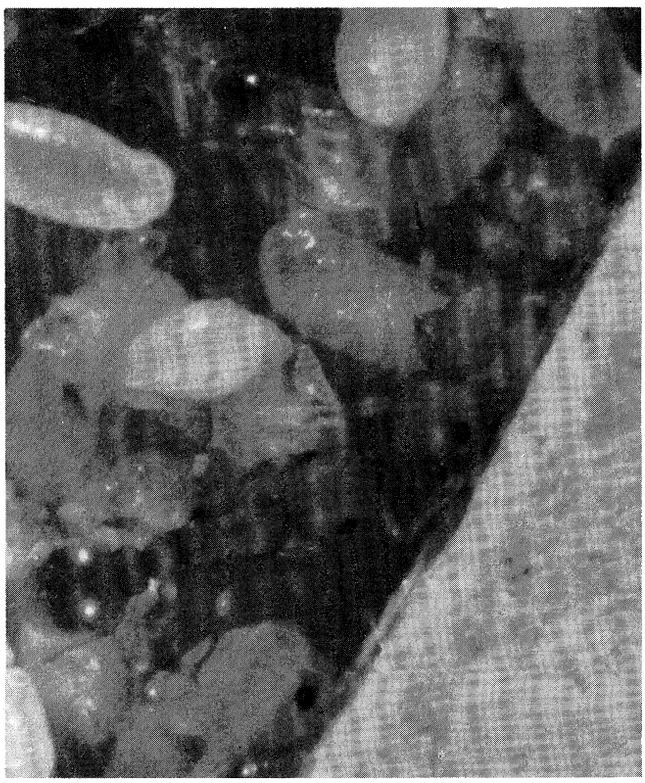

Fig. 1. Display of dominance in *Leptothorax allardycei*. The dominant is on the left (note the extended antennae) and the subordinate is on the right (note the retracted antennae and crouching posture).

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References and Notes

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2. E. O. Wilson, *The Insect Societies* [Belknap (Harvard Univ. Press), Cambridge, Mass., 1971], p. 28. While males are produced by workers in some species (*ibid.*, p. 304), there has been no suggestion of the kind of conflict between workers that I observed.
3. *Leptothorax allardycei* inhabits dead saw grass stems in pine and palmetto scrub in the Florida Keys. Colonies were collected from Sugarloaf Key and housed for observation in glass nests [E. O. Wilson, *Anim. Behav.* **24**, 354 (1976)]. The colonies were cultured in plastic containers designed to be placed on the stage of a dissecting microscope. Observations were made at ×7 to ×30 (most were made at ×10).
4. The hierarchy is apparently a modified age-graded system. [E. O. Wilson, *Sociobiology: A New Synthesis* [Belknap, (Harvard Univ. Press), Cambridge, Mass., 1975], chap. 13.
5. This is a widespread trait of dominance hierarchies (*3*). The higher the rank, the greater the effort that may be expended to defend it.
6. E. O. Wilson and T. Eisner, *Insectes Soc.* **4**, 157 (1957); E. O. Wilson, in (*2*), p. 281; B. Cole, *Insectes Soc.*, in press. Apparently only two species, *Amblyopone pallipes* and *Pogonomyrmex badius*, do not engage in oral trophallaxis.
7. Donors are easily distinguished from solicitors by a number of behavioral differences [B. Hölldobler, in *How Animals Communicate*, T. Sebeok, Ed. (Indiana Univ. Press, Bloomington, 1977), p. 418].
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10. The queen and ten workers were removed from the colony of 160 workers for 3 days and the remaining ants were fed insect remains mixed with Sudan Black [M. Brian, *Insectes Soc.* **25**, 89 (1978)]. Sudan Black is fat soluble and not transferred in liquid food exchange; thus the queen does not become contaminated with stain after she is returned to the colony.
11. The homogeneity of the individual samples was confirmed before the overall percentage was computed. The 95 percent confidence limits are 15.4 to 27.5 percent of the eggs laid. The total number of eggs counted was 187. The eggs differed developmentally from trophic eggs produced by many species [M. Brian (*10*)]. Since the queen is responsible for producing new workers in addition to virgin queens, the proportion of males produced by workers is probably much greater than 22 percent.

12. I thank E. O. Wilson, B. Hölldobler, C. Rettenmeyer, D. Wiernasz, and H. Horn for valuable comments.

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