Behav Ecol Sociobiol (1993) 33:73–77

Behavioral Ecology and Sociobiology

Nest defense and early production of the major workers in the dimorphic ant *Colobopsis nipponicus* (Wheeler) (Hymenoptera: Formicidae)

Eisuke Hasegawa

Department of Biology, Faculty of Science, Tokyo Metropolitan University, Minamiohsawa 1-1, Hachioji-si, Tokyo 192-03, Japan

Received August 20, 1992 / Accepted May 20, 1993

Summary. Production of the major subcaste and its contribution to nest survival in the dimorphic ant *Colobopsis nipponicus* was examined in the field. In this species, the first major workers were reared in the second brood, very early in the colony life cycle. A field experiment demonstrated that artificial colonies without major workers could not survive, whereas colonies with at least one major worker per nest entrance could. Because major workers of *C. nipponicus* defend the nest entrance by head plugging, the lack of nest defenders in the experimental colonies seemed to be a major cause of nest failure. The defensive value of major workers was much higher than that of minor workers. Many artificial colonies without major workers were displaced by competitors for nest sites, especially by those of other conspecific colonies. In addition, more than 90% of field colonies nested with other conspecific colonies on the same tree. The early production of major workers in *C. nipponicus* seemed to be very important for the survival of incipient colonies.

Introduction

Worker polymorphism is one of the prominent characteristics of social insects. In ants, various degrees of polymorphism have been reported for many species (see Hölldobler and Wilson 1990; Wilson 1971). Wilson (1953) classified polymorphism of ant workers into several categories using allometric criteria and discussed the evolution of worker polymorphism in ants. In his classification, complete dimorphism with two distinct subcastes is the most advanced stage. In dimorphic species, the major worker is regarded as a subcaste that specializes in several functions, such as nest defense (Detrain and Pasteels 1992; Wilson 1976), food milling (Wilson 1978) and food storage (Lachaud et al. 1992; Tsuji 1990; Wilson 1974). The division of labour among subcastes has been investigated for many species of polymorphic ants (Busher et al. 1985; Cole 1980; Mirenda and Vinson 1981; Moffet 1986, 1987; Patel 1990; Villet 1990; Wilson 1976, 1978, 1980a, b, 1984), but the studies have been limited to the aspects of caste optimization (Wilson 1980b), caste ratio regulation (Rissing 1987) and optimal caste ratio (Fowler 1987; Walker and Stamps 1986). Oster and Wilson (1978) contended that the caste system in a polymorphic species served to maximize the ergonomic efficiency of the colony. As each subcaste differs functionally, the maximization of the colony's ergonomic efficiency would be attained through the regulation of subcaste ratio. Thus, quantitative analyses of the ratio and functions of the castes are required to understand the caste system of the polymorphic species.

Colobopsis, which was recently separated from *Camponotus* as a distinct genus (Hölldobler and Wilson 1990), has dimorphic workers. The defensive behavior of its major workers is well known (Szabó-Patay 1928, cited in Wilson 1971). The major workers plug the nest entrance using the truncated head. There have been several studies of worker polymorphism in this genus (Cole 1980; Walker 1984; Walker and Stamps 1986; Wilson 1974). Walker (1984) found that small colonies of *Colobopsis impressus* invariably contained major workers. Although she pointed out the importance of their defensive role, a direct assessment of it for any species of *Colobopsis* has not yet been conducted. In this study, the timing of the production of the first major workers in the colonies was investigated in the field. In addition, I conducted a field experiment on the defensive value of the major workers. On the basis of the results, the production schedule of the major workers and the function of this subcaste were discussed.

Materials and methods

Materials and study site. C. nipponicus is a common arboreal ant in the evergreen broadleaf forests of central Japan. As in other species of *Colobopsis*, *C. nipponicus* possesses two physically distinct worker subcastes. The major workers defend their nests by plugging the entrances to it with their large truncated heads. The study site was located in a coastal forest at Amatsukominato, Chiba, Japan, where most colonies of *C. nipponicus* nest in the hollows of dead twigs attached to live trunks of the tree *Lythocarpus edulis*. Nest density was high, and several colonies could inhabit the same tree (Hasegawa 1992). From April 1990 to October 1991, a total of 542 nests were collected from 72 trees on the study site.

The collected nests were classified into 286 colonies by behavioral tests for hostility between the nest members (see Hasegawa 1992). For all colonies, the number of each subcaste was recorded. As the two worker subcastes differ markedly in size, the number of workers was not the best measure of colony size. Therefore, I used the estimated total dry weight of workers in the colony as an index of its size. The pupal dry weight of each subcaste was estimated from the regression equations of pupal weight on the number of major workers in the colony, and then the total worker weight was estimated (see Hasegawa 1993).

Field experiment. The contribution of major workers to colony persistency was examined in the field using the "pseudomutant technique" (Wilson 1980b) with a total of 150 artificial colonies. On 9 May 1991, 30 trees which had not been disturbed were selected on a ridge on the study site. Five experimental nests (see below) were attached radially to the trunk of each selected tree at a height of 1.5 m. Each experimental nest contained 30 minor workers and 20 small larvae and, in addition, each of the five colonies on the tree received 0, 1, 2, 3 or 5 major workers, respectively. These major workers originated from the same colony from which the minors and the larvae were selected. Each colony was housed in a wooden artificial nest (a hollow rectangular parallelepiped with internal dimensions of 94 (depth) × 24 (width) ×3 (height) mm and a single entrance hole (1.1 mm diameter) on one side. Each nest had a clear red plastic cover to permit observation of the activity inside the nest. A total of 150 experimental nests were set up from 41 source colonies collected in 1990. To prevent the ants from leaving their nest for a different nest on the same tree, the five nests on the same tree were established from five different colonies. The nests were inspected six times, on 31 May, 14 June, 27 June, 17 July, 7 August and 22 September 1991.

Data analyses. The field colonies whose total worker dry weight was less than 15 mg (corresponding to c. 24 minors and c. 6 majors) were assigned to the incipient stage, because most colonies below this weight contained no alates in the reproductive season (Hasegawa unpubl.). The growth of incipient field colonies was analysed by Cassie's method (Cassie 1954; cited in Southwood 1978). This method allowed the division of the incipient colonies into further subgroups, each of which had a normal distribution. Because *C. nipponicus* produces new workers annually (Hasegawa 1992), the subdivided groups can be regarded as successive cycles of brood production. Thus, the timing of the first major worker production can be determined from the appearence of the major workers in the subgroups.

When any experimental nest on a tree was replaced by another ant colony, it could be stated with certainty that competitors for the nest site were already on that tree. Thus, the classification of the experimental trees depended on whether competitors were found on the tree or not. This approach allowed me to examine the possible effects of the presence of competitors on the colony persistence in each experimental treatment. Thus, the analyses of colony persistence were conducted for two data sets based on the presence or absence of competitors on a tree.

The effect of the initial number of major workers in the experimental colonies was examined by comparing colony decrease rate in each experimental treatment. The decrease rate was defined as the number of colonies lost per day over each period between inspections. Since six inspections were conducted, six decrease rates were calculated for each treatment. This treatment obviated the problem of data dependency arising from resampling. In addition, it allowed me to compare the differences in the decrease rates according to both the experimental treatment and season.

Results

Timing of production of the first major worker

The growth of incipient colonies in the field is shown in Fig. 1. Using Cassie's method, the incipient colonies were further divided into three groups. The first group seemed to have a log-normal distribution rather than a normal distribution. However, it contained only colonies that consisted of a few minor workers (see below) and was not likely to contain two different colony groups. Thus, each group was regarded as corresponding to a cycle of brood production. Table 1 shows mean numbers of the major and the minor workers in three groups. The colonies of the first group contained minor

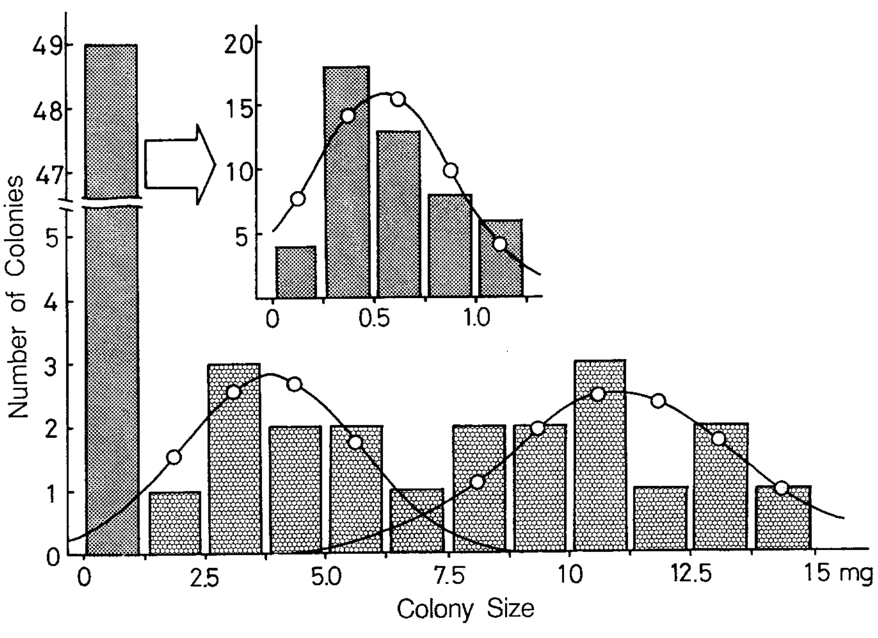

Fig. 1. Size distributions of incipient colonies of *Colobopsis nipponicus*. The *inset figure* represents the 1st group of colonies on a different ordinate scale. Three groups are recognized by Cassie's method. The *curves* represent expected normal distributions

Table 1. Numbers of minor and major workers in groups of the incipient colonies of *Colobopsis nipponicus*

	Colony group		
	1st	2nd	3rd
No. of colonies	49	9	11
No. of minors	2.3 ± 1.4	6.4 ± 6.9	18.6 ± 6.8
No. of majors	0	1.8 ± 0.9	5.0 ± 1.3

Each colony was grouped by Cassie's method. The mean and SD are shown for each group

workers only (range 1–5), whereas all colonies of the second group contained both minor (range 3–13) and major workers (range 1–4). Thus, field colonies were likely to rear the first major worker in the second brood.

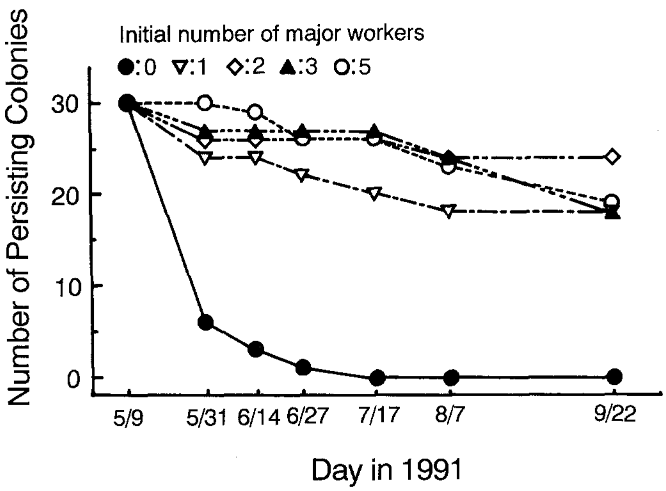

Fig. 2. The change in the number of persisting colonies in each experimental treatment during the experimental period

Significance of the major worker for colony persistence

Of the colonies without major workers, only 6 out of 30 (20%) colonies persisted to the first inspection (31 May, 22 days after the start of the experiment). Of the remaining 24 nests without majors, 2 were replaced by another ant, *Crematogaster brunnea teranishii*, and 8 nests were found vacant. The remaining 14 nests contained 2–5 *C. nipponicus* major workers. Because workers of *C. nipponicus* possess no spermatheca, the experimental colonies cannot produce female eggs. In addition, the period from the start of the experiment until the first inspection was too short to raise major workers from small larvae that were present at the start of the experiment (Hasegawa unpubl.). Therefore, these nests seemed to be occupied by members of different conspecific colonies. Moreover, these 14 colonies were maintained and contained many female larvae at the end of the experiment (22 September). This result strongly supported the conclusion that these 14 nests were replaced by conspecific colonies. In 120 colonies with majors, there was no case of replacement by other species at the time of the first inspection. Of the 120 nests 13 (10.8%) were vacant. The numbers of persisting nests in each experimental treatment, with 1, 2, 3 or 5 major workers, were 24 (80.0%), 26 (86.6%), 27 (90.0%) and 30 (100%), respectively. In all cases, the number of major workers present in the persisting colonies was unchanged or below what it was at nest initiation. This result indicated that all these colonies were persisting rather than being displaced.

Figure 2 shows the change in the number of persisting colonies during the experimental period. The experiment was ended on 22 September 1991, when the number of the minor workers in most of the persisting colonies had decreased to less than 10. All colonies without majors had disappeared by 17 July (69 days after the start of the experiment). In contrast, 65.8% (79/120) of colonies with majors persisted until the end of the experiment. In the remainder of the 40 nests with majors, 3 were replaced by other ant species (2 by *Crematogaster brunnea teranishii*; 1 by *Camponotus nawai*) and one contained a dealate *Colobopsis* queen with workers after 17 July. The latter was regarded as a replacement by a conspecific species. The remaining 37 colonies were judged to have abandoned their nests or died.

Presence of competitors on the tree and colony persistence

In the study site, 47 of 72 trees were occupied by more than one colony of *C. nipponicus*. A total of 286 colonies nested on these 72 trees. As a result, 261 of 286 (91.3%) field colonies nested with conspecific colonies on the same tree. Moreover, other arboreal ants (*Crematogaster brunnea teranishii*, *Camponotus nawai* and *Technomyrmex gibbosus*) nested on some trees that were inhabited by a single colony of *C. nipponicus*. Thus, it was concluded that many colonies of *C. nipponicus* have potential competitors for nest sites on the same tree.

As mentioned above, many nest replacements have occurred prior to the first inspection. To examine the effect of competitors on nest persistence, survival data at the first inspection are classified by the presence of competitors on the tree (Table 2). When competitors were present on a tree, all colonies without majors were replaced, whereas 62 of 64 (96.9%) colonies with majors persisted. On the other hand, 6 out of 14 (43.8%) colonies without majors and 45 of 56 (80.4%) colonies with majors persisted on trees on which no competitors were found. This difference is statistically significant ($\chi^2 = 7.964$, $P < 0.005$).

Colony persistence and initial number of majors

As demonstrated above, the presence of major workers in the colony had a strong positive effect on nest persistence when competitors were present on the same tree. However, even in the absence of competitors on the same tree, there was a significant difference in colony persistence between groups with and without majors. To eval-

Table 2. Frequencies of replaced and persisting nests on trees with and without competitive species at the time of first inspection

	Trees with competitors ($n=16$)			Trees without competitors ($n=14$)		
	Persisting	Replaced	Vacant	Persisting	Replaced	Vacant
Colonies without major workers	0/16 (0%)	16/16 (100%)	0/16 (0%)	6/14 (42.9%)	0/14 (0%)	8/14 (57.1%)
Colonies with major workers	62/64 (96.9%)	0/64 (0%)	2/64 (3.1%)	45/56 (80.4%)	0/56 (0%)	11/56 (19.6%)

uate the effects of the initial numbers of majors on colony persistency, the decrease rate was examined for each treatment. The decrease rate was not different for the six inspection periods (Kruskal-Wallis test, for trees with and without competitors, $P>0.05$). When the decrease rates for all six inspection periods were included, no difference among treatments was observed for the trees with competitors (Kruskal-Wallis test, $H=4.719$, $P>0.31$), whereas the difference in decrease rates was marginally significant in the case of the tree without competitors ($H=9.172$, $P=0.057$). Because most replacements had occurred before the first inspection, I compared the decrease rates during that period in two competitor categories. The correlation between the initial number of major workers and the decrease rate was significant on the trees without competitors (Spearman's rank correlation, $r=1.0$, $P<0.05$), but not on the trees with competitors ($r=0.5$, $P>0.05$). Thus, this suggested that the initial number of majors affects colony persistence only on the trees without competitors, especially in the early period of the experiment.

Discussion

Defensive role of the major workers

The competiton for nest sites is reported to be severe in arboreal ant species Herbers (1989). Yamaguchi (1992) found that many nests of the cavity-using ant *Leptothorax congruus* are usurped by *Monomorium intrudens*. Herbers (1986) showed that nest demography of *L. longispinosus* is affected by the addition of nest materials to the study field. She argued that this change was caused by the relaxation of nest site limitations on the site. These two studies indicate that in arboreal ant communities there is both inter- and intraspecific competition for the nest site.

The present study demonstrates that presence of major workers has a strong positive effect on nest persistence in *C. nipponicus*. Before the first inspection, all colonies without majors on trees with competitors were replaced, mainly by the conspecific colonies, whereas the nests of many colonies with majors on the same tree persisted during the same period. Thus, intraspecific competiton was most intense, and the lack of nest defenders (major workers) appeared to be the major reason for the difference in nest persistence. There is, however, a significant difference of the colony persistence rate between the two types of colonies on the trees without competitors. In addition, the decrease rate of colonies seemed to be correlated with the initial number of majors in such trees. Since the major workers of *C. nipponicus* specialize in nutrition storage in their gaster (Hasegawa 1993), some factors other than colony defense, such as nutritional support to other colony members, may be involved. However, at the study site, more than 90% of the field colonies nested with potential competitors on the same tree. Thus, if major workers are absent from the nest, the colony cannot persist.

A single major worker had a strong positive effect on nest persistence. In the field, I often observed that a major worker plugged the single entrance hole of an experimental nest. When any competitors try to usurp a *Colobopsis* nest, they can assess the defensive ability of the resident *Colobopsis* colony only by the nest defenders (major workers) at the nest entrances. The fact that a single major is sufficient for the defence of a experimental nest that has a single entrance may explain the lack of correlation between the initial number of major workers and the decrease rate of colonies over the experimental period.

Early production of major workers

In polymorphic ant species, major workers generally appear in well developed colonies (Gibson 1989; Ito et al. 1988; Porter and Tschinkel 1985; Tschinkel 1988; Wilson 1983). It seems, however, that *C. nipponicus* rears its first major workers from an early (second) brood in the field. At that stage, the colonies contain 3–13 minors and 1–4 majors, whereas a foundress of *C. nipponicus* produces 1–5 individuals of only the minor subcaste. The average dry weight of a major worker is three times that of a minor worker (Hasegawa 1993). Hence, if the queen rears a major worker in the first brood, the colony would lack foraging minors and could not survive. Walker (1984) found that small colonies of *Colobopsis impressus* invariably contained a few major workers. She argued that early production of major workers reduces the risk to the colony queen that would otherwise have to participate in the defense of the nest, if the major workers were absent. In this study, competition for the nest sites was most intense among conspecific colonies. In the laboratory, a colony without majors was invaded by another colony that robbed the brood of the former (Hasegawa pers. obs.). At the study site, more than 90% of the field colonies had potential competitors on the same tree. Thus, early production of major workers would considerably reduce the risk of nest usurpation and subsequent demise of the colony.

Besides *C. nipponicus*, early production of a few large workers (or soldiers), had been observed in the ant *Camponotus nawai* (T. Satoh pers. comm.), and in the damp wood termite *Hodotermopsis japonica* (Hirono 1990). These two species also nest in plant cavities and, in the case of *C. nawai*, plugging behavior by large workers was seen in the field (T. Satoh pers. comm.). Thus, in polymorphic social insects, knowledge of caste functions is important in understanding the development schedule of colonies because it may be optimized for colony survival in addition to the optimization of numerical ratios among the subcastes (Oster and Wilson 1978).

Acknowledgements. I thank Dr. K. Miyashita for his encouragement and help with this study. I am grateful to Drs. T. Suzuki, T. Kusano, T. Asami, T. Satoh and K. Masuko for invaluable comments on the early versions of the manuscript. I also acknowledge M. Terayama for identification of specimens. Two anonymous referees also provided many helpful suggestions for improvement of the manuscript.

References

Busher CE, Calabi P, Traniello JFA (1985) Polymorphism and division of labor in the neotropical ant *Camponotus sericeiventris* Guerin (Hymenoptera: Formicidae). Ann Entomol Soc Am 78:221–228

Cole BJ (1980) Repertoire convergence in two mangrove ants, *Zacryptocerus varianus* and *Camponotus (Colobopsis)* sp. Insectes Soc 27:265–275

Detrain C, Pasteels JM (1992) Caste polyethism and collective defense in the ant, *Pheidole pallidura*: the outcome of quantitative differences in recruitment. Behav Ecol Sociobiol 29:405–412

Fowler HG (1987) Worker polymorphism in field colonies of carpenter ants (Hymenoptera: Formicidae: *Camponotus*): Stochastic selection? Insectes Soc 34:204–210

Gibson RL (1989) Soldier production in *Camponotus novaeboracensis* during colony growth. Insectes Soc 36:28–41

Hasegawa E (1992) Annual life cycle and timing of male egg production in the ant *Colobopsis nipponicus* (Wheeler). Insectes Soc 39:439–446

Hasegawa E (1993) Caste specialization in food storage in the dimorphic ant *Colobopsis nipponicus* (Wheeler). Insectes Soc 40, in press

Herbers JM (1986) Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. Behav Ecol Sociobiol 19:115–122

Herbers JM (1989) Community structure in north temperate ants: temporal and spatial variation. Oecologia 81:201–211

Hirono Y (1990) Histological and ecological studies on the caste differentiation of the Japanese damp-wood termite *Hodotermopsis japonica* (Termopsidae: Isoptera). Doctor's thesis, University of Tokyo, Tokyo, Japan

Hölldobler B, Wilson EO (1990) The ants. Belknap, Cambridge

Ito F, Higashi S, Maeta Y (1988) Growth and development of *Camponotus (Paramyrmamblys) kiusiuensis* Santschi colonies (Hymenoptera Formicidae). Insectes Soc 35:251–261

Lachaud JP, Passera L, Grimal A, Detrain C, Beugnon G (1992) Lipid storage by major workers and starvation resistance in the ant *Pheidole pallidula* (Hymenoptera, Formicidae). In: Billen J (ed) Biology and evolution of social insects. Leuven University Press, Leuven, Belgium, pp 153–160

Mirenda JT, Vinson SB (1981) Division of labour and specification of castes in the red imported fire ant *Solenopsis invicta* Buren. Anim Behav 29:410–420

Moffet MW (1986) Notes on the behavior of the dimorphic ant *Oligomyrmex overbecki* (Hymenoptera: Formicidae). Psyche 93:107–116

Moffet MW (1987) Division of labour and diet in the extremely polymorphic ant *Pheidologeton diversus*. Nat Geog Res 3:282–304

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Patel AD (1990) An unusually broad behavioral repertory for a major worker in a dimorphic ant species: *Pheidole morrisi* (Hymenoptera: Formicidae). Psyche 97:181–191

Porter SD, Tschinkel WR (1985) Fire ant polymorphism (Hymenoptera: Formicidae): factors affecting worker size. Ann Entomol Soc Am 78:381–386

Rissing SW (1987) Annual cycles in worker size of the seed-harvester ant *Veromessor pergandei* (Hymenoptera: Formicidae). Behav Ecol Sociobiol 20:117–124

Southwood TRE (1978) Ecological methods. Chapmann and Hall, New York

Tschinkel WR (1988) Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. Behav Ecol Sociobiol 22:103–115

Tsuji K (1990) Nutrient storage in the major workers of *Pheidole ryukyuensis* (Hymenoptera: Formicidae). Appl Entomol Zool 25:283–287

Villet MH (1990) Division of labour in the Metabele ant *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae). Ethol Ecol Evol 2:397–417

Walker JM (1984) The soldier caste and colony structure in the ant *Camponotus* (Colobopsis) *impressus*. Dissertation, University of California, Davis, California, USA

Walker JM, Stamps J (1986) A test of optimal caste ratio theory using the ant *Camponotus (Colobopsis) impressus*. Ecology 67:1052–1062

Wilson EO (1953) The origin and evolution of polymorphism in ants. Q Rev Biol 28:136–156

Wilson EO (1971) The insect societies. Belknap, Cambridge

Wilson EO (1974) The soldier of the ant *Camponotus (Colobopsis) fraxinicola* as a trophic caste. Psyche 81:182–188

Wilson EO (1976) A social ethogram of the neotropical arboreal ant *Zacryptocerus varianus* (Fr. Smith). Anim Behav 34:354–363

Wilson EO (1978) Division of labour in fire ants based on physical castes (Hymenoptera: Formicidae: *Solenopsis*). J Kansas Entomol Soc 51:615–636

Wilson EO (1980a) Caste and division of labour in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) I: The overall pattern in *A. sexdens*. Behav Ecol Sociobiol 7:143–156

Wilson EO (1980b) Caste and division of labour in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) II: The ergonomic optimization of leaf cutting. Behav Ecol Sociobiol 7:157–165

Wilson EO (1983) Caste and division of labour in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) IV: Colony ontogeny of *A. cephalotes*. Behav Ecol Sociobiol 14:55–60

Wilson EO (1984) The relation between caste ratios and division of labour in the ant genus *Pheidole* (Hymenoptera: Formicidae). Behav Ecol Sociobiol 16:89–98

Yamaguchi T (1992) Interspecific interference for nest sites between *Leptothorax congruus* and *Monomorium intrudens*. Insectes Soc 39:117–127