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THE BIOLOGY OF THE PRIMITIVE ANT *ANEURETUS SIMONI* (EMERY) (FORMICIDAE : ANEURETINAE)

II. THE SOCIAL ETHOGRAM AND DIVISION OF LABOR

J.F.A. TRANIELLO (1), A.K. JAYASURIYA (2)

(1) Boston University, Department of Biology, Boston, Massachusetts 02215, U.S.A.
(2) Harvard University, Museum of Comparative Zoology Laboratories, Cambridge, Massachusetts 02138, U.S.A.

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SUMMARY

Social behavior in *Aneuretus simoni* is quantitatively described in a social ethogram. The majority of acts exhibited by queens and minor and major workers are typical behaviors observed in species of the higher subfamilies of ants.

A Fagen-Goldman analysis of the frequency of behavioral acts indicated that the observed repertory was complete. Observed repertory sizes were 5 acts (the queen), 14 acts (major workers), 28 acts (callow minor workers) and 31 acts (mature minor workers). These repertory sizes are comparable to those observed in other ant species.

Major workers, which average less than two in number per colony, do not show brood care. Majors were also never observed to participate in colony defense. The behavioral repertory of callow minor workers includes queen-related acts, brood care, and foraging.

A comparison of social organization in *A. simoni* and other so-called primitive and advanced species indicates that social behavior is very similar to that of dolichoderine species.

RESUME

Biologie de la fourmi primitive Aneuretus simoni **(Emery) (Formicidae : Aneuretinae)**

II. Ethogramme social et division du travail

Nous décrivons quantitativement l'organisation sociale chez *Aneuretus simoni* avec un éthogramme social. La majorité des comportements des reines et des petites et grandes ouvrières est semblable à ceux des espèces de fourmis des sous-familles supérieures.

L'analyse de Fagen-Goldman des fréquences des comportements montre que le répertoire observé était complet. Les tailles des répertoires étaient 5 comportements (reine), 14 comportements (grandes ouvrières), 28 comportements (petites ouvrières jeunes), et 31 comportements (petites ouvrières mûres). Ces tailles de répertoires sont comparables à celles d'autres espèces de fourmis.

Les grandes ouvrières, dont on trouve seulement moins de deux en moyenne par colonie, ne montrent pas de comportements de soins envers les larves. Elles ne montrent pas de comportements défensifs. Les ouvrières jeunes montrent les comportements envers la reine, les larves, et aussi le comportement de récolte.

Une comparaison de l'organisation sociale chez *Aneuretus simoni* avec celle d'autres espèces primitives montre que le comportement social est semblable à celui des dolichodérines.

INTRODUCTION

The recent collection of queenright colonies of *Aneuretus simoni* has made it possible to study social organization in this rare ant species for the first time since the initial studies of Wilson *et al.* (1956), 29 years ago. Our previous reports on the distribution, abundance and foraging behavior of *A. simoni* on Sri Lanka (Jayasuriya and Traniello, 1985 a), and on alarm and trail communication in this species (Traniello and Jayasuriya, 1981 a, b) have provided considerable information on the ecology and social biology of this elusive, primitive ant species, which is the sole living representative of the subfamily Aneuretinae.

To further contribute to the comparative sociobiology of primitive ant species and the study of the evolution of sociality in ants in general, we present in this paper the social ethogram of *A. simoni* and describe patterns of division of labor by physical caste and age.

METHODS

Twenty-six colonies of *A. simoni*, collected on Sri Lanka in July 1979, were housed in glass tubes that approximated the size and structure of their natural twig nests (10 cm in length, 0.5 cm in diameter) to facilitate observation. Each tube was fitted with a moist cotton plug which could be periodically dampened with water. These nests were placed in fluon-lined plastic containers (12.5 × 18 × 6 cm) small enough to be fitted onto the stage of a dissecting microscope. The nest container served as a foraging arena, in which termites (*Nasutitermes* spp.), and honey water were offered as food. With this observation technique the entire population of a colony could be monitored. A low intensity fiber optics cold light source was used to minimize disturbance. Observations were made at magnifications ranging up to 30x. The majority of observations were made on three vigorous queenright colonies that survived more than nine months in the laboratory. The paucity and fragility of *A. simoni* colonies have somewhat constrained the scope of our experimentation. Nest containers were covered and misted with water to maintain humidity, and room temperature ranged from 28° - 30°.

A total of 53.6 hours were devoted to observing two queenright colonies and 4,105 separate behavioral acts were recorded. Each observation period averaged 4-5 hours, and equal time was spent scan sampling the behaviors of ants inside and outside the nest in the manner described by Wilson and Fagen (1974). Behavioral frequency data were similar in both colonies, and any differences appeared to reflect only colony size and population. Data were pooled to provide a more accurate description of species-typical patterns and to increase sample sizes. Behaviors were described according to consequence. For grooming and trophallaxis, the identity of the individual performing the act (grooming another individual or donating food) was recorded.

Observations were made randomly throughout the day in four —to five — hour periods to avoid a bias resulting from diurnal variation in behavior. Data were collected over a two-week period. Repertoires were analyzed for completeness according to the methods described by Fagen and Goldman (1977), fitting behavioral frequency data to negative binomial and lognormal Poisson distributions.

Additional methodological details will be given concurrently with the description of experiments in the text.

RESULTS

Description of behavioral acts

The social ethogram of *A. simoni* is presented in *table I*, in which the behavioral frequency data recorded for two colonies are combined. Of the behavioral acts recorded, some are worthy of description and discussion.

Egg laying (behavior number 10)

In colony 1, of the two dealate females, one was observed laying on several occasions while the other was seen laying only one egg. Although the eggs of both females appeared identical and were handled similarly by the attendant workers, it is not absolutely certain that the colony was truly polygynous. It is possible that one of the dealate queens laid trophic or infertile eggs. No aggression between queens was observed in any colony with more than one dealate female. Neither the consumption of trophic eggs nor worker egg-laying was seen, although dissection of callow workers from both queenright and queenless colonies revealed ovaries containing well developed eggs. The presence of yolk remnants in mature workers that eggs are eventual resorbed.

Removing freshly laid egg from queen (behavior number 11)

The queen is not assisted during the egg-laying process. Once the entire egg has emerged, it is removed by a worker and placed in a pile with other eggs. The eggs are highly adhesive, unlike those of other primitive genera.

Table I. — Relative frequencies of behavioral acts according to caste in *Aneuretus simoni*. N = total number of behavioral acts recorded for eache caste. Data from two colonies were pooled.

Tableau I. — Fréquences relatives des comportements suivant la caste chez *Aneuretus simoni*. N = nombre des comportements dans chaque caste. Les données de deux colonies sont combinées.

Population data on the colonies observed :

	queens	minor workers mature	minor workers callow	major worker	eggs	larvae	pupae
Colony 1	2	96	9	2	308	11	5
Colony 2	1	64	12	3	53	32	14

Behavior	Minor workers		Major worker (N = 131)	Queen (= 35)
	Mature (N = 3176)	Callow (N = 763)		
Grooming :				
1. Self-groom	.3315	.1467	.1756	.0571
2. Allogroom mature minor	.0957	.0366	.0458	0
3. Allogroom callow	.0075	.0157	.0611	0
4. Allogroom major	.0050	.0026	0	0
5. Allogroom queen	.0085	.0262	0	0
Trophallaxis :				
6. with mature minor	.0724	.0353	.1450	.6857
7. with callow	.0072	.0104	.0687	.0571
8. with major	.0059	.0026	0	0
9. with queen	.0075	.0117	0	0
Brood related :				
10. Lay egg	0	0	0	.1714
11. Remove freshly laid egg frim queen	.0015	.0026	0	0
12. Carry or roll egg(s)	.0818	.0760	0	0
13. Lick egg(s)	.0195	.1100	0	0
14. Carry or manipulate larva	.0702	.0891	0	0
15. Carry larva to food	.0097	.0288	0	0
16. Lick larva	.0226	.0615	0	0
17. Regurgitate to larva	.0103	.0865	0	0
18. " Rescue " egg from larva	0	.0013	0	0
19. Assist larval ecdysis	.0006	.0026	0	0
20. Assist pupation	0	.0052	0	0
21. Carry or manipulation pupa	.0579	.0668	0	0
22. Assist eclosion	.0009	.0157	0	0
23. Carry pupal/larval skin	.0059	.0131	0	0
24. Clean brood chamber	.0195	.0366	.0001	
Foraging :				
25. Forage outside of nest	.0302	.0222	.1221	0
26. Feed on sugar water (outside of nest	.0327	.0249	.0534	0
27. Feed on insect prey outside of nest	.0050	0	0	0
28. Lay trail to food source	.0097	.0026	.0229	0
29. Retrieve insect prey	.0103	.0002	.0021	0
30. Feed on insect prey inside nest	.0223	.0550	.1221	0
Miscellaneous :				
31. Repair nest	.0176	.0104	0	0
32. Adult transport	.0129	0	.0229	0
33. Necrophoresis	.0119	0	.1374	0
34. Mechanically display to nest mate	.0044	0	.0229	0
35. Graze larvae	0	0	0	.0285
TOTAL	1.0	1.0	1.0	1.0

Licking larvae (behavior number 16)

Larvae are constantly groomed by the workers. There appears to be a slight preference for the head region and it is possible that some secretion is exuded by the larvae (see " grazing larvae " below).

" Rescuing " egg from larva (behavior number 18)

A worker was seen pulling an egg away from a larva in a colony that had not been fed for three days. This was a rare occurrence and on no other occasions, not even under conditions of semi-starvation, was any form of cannibalism observed.

Carrying larvae to food (behaviour number 15)

The *Aneuretus larvae* are not able to crawl unaided to food, as reported in the primitive genera *Nothomyrmecia* (Taylor, 1978), *Amblyopone* (Haskins, 1928 ; Traniello, 1982) and *Myrmecia* (Haskins and Haskins, 1950). However, they feed directly upon fresh insect (*Drosophila*) fragments. The workers carry the larvae directly to the prey or offer them small fragments.

Assisting pupation and eclosion (behavior number 20)

Worker assistance in pupation and eclosion is considered an advanced trait (Wilson, 1971). Prior to pupation, the larva is thoroughly licked : one worker holds the larva in place while approximately four other workers groom it. Next, the larva is covered with soil particles which serve as anchor points for silk, thus aiding it in spinning its cocoon. An unusual feature is the use of eggs and small larvae for banking a spinning larva. Whether this was accidental, that is, whether the eggs and small larvae stuck to the spinning larvae due to their adhesiveness, or whether this is a novel use of brood, is unclear. Moreover, the larvae pupate clumped together in groups of two or three. This may also facilitate anchorage for spinning. After about four hours, when the cocoons are complete, workers remove the debris, separate the pupae, and carry them to a certain area of the nest where they remain until eclosion.

As the pupae near eclosion, the fully metamorphosed and lightly pigmented adult is visible through the transparent covering. Workers aggregate around the eclosing individual and make vigorous antennal contact. Soon, small incisions in the cocoon are made, and workers extract the callow adult. The pupal skin is then removed. As in formicines, callows are extremely pale, soft and immobile, and more than a day is required for these callows to be capable of performing tasks in

the colony. The legs and antennae of the newly eclosed callows which are initially folded in pupal posture, are stretched out and the young are groomed profusely. This is in sharp contrast to adult eclosion in the primitive ponerine genus *Amblyopone*, in which the young insect gnaws its way out of the cocoon unaided, and is able to assume active colonial duties almost immediately afterwards (Haskins, 1928 ; Traniello, 1978). Stuidies on *Myrmecia* reveal an intermediate situation : eclosion is partly aided but can occur unaided as well ; the callows are not immediately active, but require only several hours to gain competence (Haskins and Haskins, 1950). Thus, with respect to eclosion, *Aneuretus* behavior is similar to that of the advanced ants.

On rare occasions, however, immature forms are seen lying naked on the nest floor. These probably result from premature removal of the cocoon, similar to that reported in *Myrmecia* by Haskins (1950).

Grazing of larvae (behavior number 35)

This behavior was observed only on one occasion, in a colony that had been starved for three days. The queen was seen licking liquid material from the region of the larval mouthparts, similar to the behavior reported by Wilson (1974) in *Leptothorax curvispinosus*. The queen's mandibles remained closed, while the glossa was moved over the larval mouthparts. Thus, the larva did not seem to be regurgitating to the queen as observed in *Amblyopone pallipes* (personal observations). The nature of the liquid collected from the larva by the queen is uncertain, but is presumably labial gland secretion (Wilson, 1974). It is possible that the same is true of *Aneuretus*. As already noted, the grooming workers also show some preference for the head regions of the larvae. Whether they are simply grooming the larvae or receiving nutrition is not clear.

Analysis of repertory size and completeness

During the 53.6 hours of observation, a total of 4,105 acts of 35 categories were recorded. The frequency data (number of acts observed per category) for each caste and subcaste were fitted to a lognormal Poisson distribution which was found to fit the data much better than a negative binomial distribution. The sample coverage, defined as P_i where P_i is the probability of performance of each observed act i, was also calculated. In major workers and queens, the abundance of rare acts was an obvious indication of repertory incompleteness. Results are presented in *table II*.

The number of behavioral acts in the minor worker repertory was estimated to be 32, with a 95 % confidence interval of (29,34). This

Table II. — Summary of the analysis of the social ethogram of *Aneuretus simoni*. The estimated repertory size, the 95 % confidence interval and sample coverage were calculated by fitting the observational data to a lognormal Poisson distribution.

Tableau II. — Résumé de l'analyse de l'éthogramme social chez *Aneuretus simoni*. La taille estimée du répertoire, l'intervalle de confiance 95 %, et champ d'application d'échantillon sont calculés en accord avec la méthode de FAGEN et GOLDMANN (1977).

Caste or subcaste	No. of acts observed	Observed repertory size	Estimated repertory size	95 % confidence interval	Sample coverage
Mature Minor Worker	3176	31	31.8	[29,34]	100 %
Callow Minor Worker	763	28	28.8	[25,30]	99,7 %
Major Worker	131	14	14.5	[13,15]	100 %
Queen	35	5	5.4	[5,6]	99.7 %

estimated repertory size is comparable to that of the worker caste of monomorphic *Leptothorax* species (Wilson and Fagen, 1974), and of the minor worker subcastes of *Zacryptocerus varians* (Wilson, 1976 a) and *Pheidole dentata* (Wilson, 1976 b).

Division of labor by physical caste

The worker caste of *A. simoni* is completely dimorphic (Wilson *et al.*, 1956). The primary morphological difference between the major and the minor is the major's proportionately larger and broader head, but the behavioral difference between *Aneuretus* majors and minors have not previously been studied. In seven queenright colonies collected, major workers ranged from only one to three in number per colony (1.7 ± 0.8, mean ± s.d.), whereas minor workers, ranging from 18 — 106 per colony (mean = 65.4 ± 28.7) comprised the majority of the worker caste and attended to the colony's labor requirements (Jayasuriya and Traniello, 1985).

The ethogram presented in *table I* shows that, consistent with results in other polymorphic species, *Aneuretus* majors have a more limited repertory (14 acts) than that of minor workers (31 acts).

The most prominent feature of the behavioral repertory of the major worker caste is the absence of brood care, a pattern similar to other completely dimorphic ant species of the more advanced subfamilies. However, unlike the major workers of other dimorphic ants,

major workers showed no defensive specialization in any context. They did not consistenly occupy what could be interpreted as guarding positions at the nest entrance. When individuals from a foreign *A. simoni* colony were placed in the arena of a given colony, the normally timid workers attempted to bite and sting the intruders and the pair sometimes remained locked in combat for hours, but majors were not recruited (Jayasuriya, 1980). Assaulting colonies with workers of sympatric ant species (*Pheidole hortensis, Tetramorium* sp.) was also ineffective in inducing the participation of majors in defense. In response to disturbance (prodding at the nest entrance with an applicator stick) minor workers responded aggressively whereas major retreated. Observations made during nest emigration indicate a high of major worker participation (brood and worker transport) during this process. Majors possess a well-developed sternal gland (Traniello and Jayasuriya, 1981 a) and therefore could contribute to the chemical organization of nest moving. If nest immigration plays a central role in the biology of *Aneuretus,* this could comprise a significant part of the major worker behavioral repertoire.

Division of labor by age

In addition to the major worker/minor worker subcaste distinction, callow minors (less than 8 days old), recognized by their pale coloration, were considered as a potential age caste and the behavioral distinctiveness of this age group was examined. We were unable to make any finer discrimination of worker age due to the lack of sufficient additional heterogeneity in color. To analyze age-based division of labor, the frequencies of task performance by callow and mature workers expected from their numerical frequencies in the colonies observed were calculated using the method of Altmann and Altmann (1977), applied to the analysis of age polyethism by Calabi *et al.* (1983) :

$$E_{ij} = \frac{(B_i)(n_j)}{N}$$

where E_{ij} = expected frequency of behavior $_i$ by age class $_j$

B_i = observed frequency of behavior $_i$ by all age classes

n_j = number of ants in age class $_j$

N = total number of ants in all age classes.

We analyzed the differences between callow and mature minor workers in their performance of behaviors frequently observed inside the nest related to queen attendance and brood care, and behaviors outside of the nest involving foraging, as well as nest maintenance.

Table III. — Age-based division of labor in *A. simoni*. Numbers below description of behaviors correspond to those in Table 1. No = number of acts observed ; Ne = number of acts expected based upon frequency of caste in colony ; Fo = observed frequency of acts ; Fe = expected frequency of acts. Statistical analysis based on χ^2 test.

Tableau III. — Le polyéthisme chez *A. simoni*. Les numéros des comportements correspondent au Tableau 1. No = nombre de comportements observés ; Ne = nombre d'actes théorique en fonction de la fréquence de la caste ; Fo = fréquence observée des comportements ; Fe = fréquence théorique des actes. Analyse statistique par un test χ^2.

Behaviors	Mature minor workers				Callow minor workers				χ^2	Significance of difference
	No	Ne	Fo	Fe	No	Ne	Fo	Fe		
Queen-related acts (5,9,11)	56	76.9	.6437	.8839	31	10.1	.3563	.1161	48.9	$p << .001$
Brood care (12 - 17 ; 19 - 23)	889	1142.9	.6875	.8839	404	150	.3125	.1160	486.4	$p << .001$
Foraging-related acts (25 - 30)	351	381.9	.8125	.8840	81	50.1	.1875	.1160	21.6	$p < .001$
Nest maintenance (24,31)	118	136	.7662	.8831	36	17.9	.2338	.1162	20.7	$p < .001$

Results (*table III*) show that callow minor workers perform queen-associated behaviors and brood care tasks at rates that are 3.2 and 2.7 times greater, respectively, than the performance frequency predicted from the number of callows present in the colonies observed. Mature minor workers perform these same tasks at rates of 0.73 and 0.78 of their expected frequencies, respectively, and therefore participate in queen-associated acts and brood care significantly less than callows. There are also significant differences between young and old workers in the relative performance of foraging-related tasks and nest maintenance. Mature workers engage in these behaviors at 0.92 and 0.87 times their expected frequencies, respectively, whereas callow minors are unusually active in the performance of these tasks, contributing 1.6 and 2.0 times more labor, respectively, than predicted from the number of callows present in *A. simoni* colonies.

DISCUSSION

Few species of ants are of equal importance to *Aneuretus* for the study of social evolution in the Formicidae, yet the behavior of *A. simoni* has been known only from scant observations. Wilson *et al.* (1956) described the morphology and ecology of *A. simoni* based on a collection of 20 colonies, of which only two were queenright. Behavioral notes were restricted to foraging habits, larval provisioning and trophallaxis. Our present study represents the first quantitative analysis of social organization in *A. simoni,* and several features of its social behavior revealed in this study merit discussion in light of social evolution in ants, and the common reference to *Aneuretus* as a primitive ant.

Perhaps the most singularly striking finding is that social structure in *A. simoni* is surprisingly similar to that of ants in the higher subfamilies. The observed repertory of *A. simoni* includes 35 behavioral acts that are common in ants, and ant repertory size is similar to that obtained for other species (Fresneau *et al.*, 1982 ; reviewed in Calabi *et al.*, 1983 ; Herbers, 1983). Minor workers of *A. simoni* exhibited 31 acts, and although this represents a large repertory size, it is not unusual in light of the results of studies on other polymorphic species (e.g. Wilson, 1976 a, b). Moreover, the types of acts in the minor worker repertory in *A. simoni* overlap considerably with those of other species of ants such as *Pheidole, Solenopsis, Leptothorax, Formica,* and *Zacryptocerus* (reviewed in Oster and Wilson, 1978 ; Fresneau *et al.*, 1982 ; Herbers, 1983 ; Calabi *et al.*, 1983).

Social behavior in *A. simoni* is comprised of a number of behaviors which, like other primitive ant species, represent a blend of advanced

and primitive characteristics. One of the most prominent primitive characteristics is the use of the well-developed exsertile sting to paralyze prey. When live termites were offered in the foraging areas of colonies, minor workers would without assistance grasp, sting, and retrieve them to the nest. The termite could be observed making " twitching " movements suggestive of paralysis as it lay within the nest. Workers and larvae consumed prey within a few days. Another primitive behavior related to brood care is the habit of provisioning larvae with prey fragments. Prey are dismembered by workers within the nest, and pieces of prey are placed close to larvae. Unlike the primitive genera *Myrmecia* and *Amblyopone, A. simoni* larvae are motile and are not able to move to the prey to feed (Haskins, 1928 ; Haskins and Haskins, 1950 ; Traniello, 1982). Nourishment of larvae also includes regurgitation of liquid food from workers, a social behavior absent in *Myrmecia* and *Amblyopone,* among other primitive species. As is also the case in *Amblyopone* and *Myrmecia,* mature *A. simoni* larvae are banked with soil prior to pupation. The soil particles appear to serve as anchoring points for silk ; following the completion of the pupal case, workers remove the debris. Eclosion from the pupal case only occurs with the assistance of workers, which cut the pupal case with their mandibles and pull the callow individuals within free of the exuvia. Given that this is a trait found in species of the advanced subfamilies, brood care acts, taken together, include ancestral and advanced social features.

The most unusual aspect of the social behavior of *A. simoni* is in the pattern of age and size based division of labor. On the average, only 2.4 % of the worker population of a colony is composed of majors, and the maximum number of majors present in any queenright colony ($N = 7$) or queenless colony ($N = 19$) was three. It seems unlikely that such a small number of majors could effectively serve as defensive specialists. Indeed, our observations do not suggest a protective function. Given their broad heads and relatively narrow entrances to their nests in twigs, they seem adapted to serve as nest guards, yet major worker guarding was not consistently observed and majors were also often observed at the far end of the nest. We observed that majors feed avidly on honey water and insect prey, at times resulting in a swelling of the gaster to the point of exposing the intersegmental membranes. Majors also show a high frequency of regurgitation with both mature and callow workers, and because trophic behaviors constitute 65 % of the frequency of acts in their repertory (exclusive of self grooming), they may play a role in food storage, as do the major workers of other ant species (Wilson, 1974 ; Calabi *et al.,* 1983). Also, because we did not observe any callow major workers in any colony, it is possible that, when young, they care for brood. It is difficult to interpret whether the lack

of readily observable task specialization by major workers and their low numerical frequency suggest the beginnings of polymorphism, the presence of a relic caste, or an optimal caste ratio for the relatively small *A. simoni* colonies.

The pattern of age polyethism in *A. simoni* appears to represent an incipient phase of division of labor in ants. Young workers are to a limited extent specialists at queen-related and brood care tasks, but also perform tasks such as foraging that are characteristic of the repertories of older workers (Oster and Wilson, 1978). Callow and mature minor worker labor profiles overlap considerably, especially in regard to nest maintenance and foraging-related tasks. This pattern contrasts with the lack of age polyethism shown in other primitive species such as *Amblyopone pallipes* (Traniello, 1978), *Nothomyrmecia* (Holldobler, personal communication), and *Myrmecia* (Haskins and Haskins, 1950). The generalized behavioral repertory of callow minor workers may be due to the fact that in *A. simoni* larvae are directly provisioned with insect prey; therefore, the typically unrelated tasks of foraging and larval provisoning are part of the same behavioral sequence. However, the commencement of foraging by callows during their first few days of adult life seems to be a truly ancestral trait, especially in view of the small number of callow workers in a colony. A more detailed analysis of age polyethism in *A. simoni* is in preparation.

Social behavior in *A. simoni* is basically quite similar to descendant dolichoderine species, and is very different from other primitive species with small colonies such as *Amblyopone* (Haskins, 1928; Traniello, 1982), *Myrmecia* (Haskins and Haskins, 1950) and *Nothomyrmecia* (Holldobler and Taylor, 1983). For example, trophallaxis is quite common, and trail communication, movement of workers between nests, rapid, chemically-organized nest emigration, and group retrieval of prey are prominent features of the foraging behavior of *A. simoni* in the field and in the laboratory. The pattern of nest emigration is very similar to that of ants of the higher subfamilies in which after an initial group of approximately 20-30 nestmates are recruited to the new nest site, the number of nestmates arriving at the new nest increases by social carrying (Jayasuriya, 1980). In *A. simoni*, adult transport begins with a brief interchange of invitation signals inducing tonic immobility in the individual to be carried. A worker is then grasped by the mandibles and carried over the transporter's head. The social transport posture in *A. simoni*, therefore, is clearly more advanced than in other primitive species and is most similar to that of the higher ponerines and myrmicines. Social carrying has not been observed in the Dolichoderinae (Wilson, 1971).

In apparently polygynous colonies of *A. simoni* no aggression or dominance relationships occur between queens, as is true in *Nothomyr-*

mecia (Hölldobler and Taylor, 1983). Dissections of workers indicate ovarian development is reduced in mature individuals. Although queen/queen aggression was not observed, in a colony with two queens workers were seen attacking one queen, which was eventually dragged out of the nest. Subsequent attempts to reintroduce the queen consistently resulted in aggression by workers. These observations suggest a queen-reduction process similar to what has been described in other ant species. Additional studies on colony foundation are required before the significance of this behavior can be determined.

The results of our recent studies on *A. simoni*, the new information made available on *Nothomyrmecia* since its rediscovery by Taylor (1978), and the results of numerous other studies on primitive ant species (Fresneau *et al.*, 1982) suggest that myrmecologists may not find more information on the nature of sociality that evolved in the history of the Formicidae than is already available in the above cited research. Although certain ancestral traits can be easily identified in so-called primitive ants, it appears that the *basic* theme of sociality in these species reflects the social behavior of ants of the higher subfamilies. In particular, this seems to be true of *Aneuretus*.

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