FORAGING AND MORPHOLOGY IN ANTS : THE ROLE OF VERTEBRATE PREDATORS AS AGENTS OF NATURAL SELECTION

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SUMMARY

Most recent studies concerning the ecology of foraging in ants have emphasized only the relationship between ants and their food resources. Though mainly speculative, this contribution suggests that ants' predators, notably lizards and anurans, may have had great importance in the morphological evolution and the ecology of foraging in ants. A simple theoretical model of the ecology of foraging is used to suggest some possible evolutive results as a consequence of predation. Data obtained on foraging ants on Barro Colorado Island, Panama, support some of these suggestions. Finally, a checklist of the possible evolutive results of predation on foraging ants is presented.

RESUMEN

Forrajeo y morfologia de las hormigas : papel de los Vertebrados depredadores como factores de seleción natural.

La mayoría de los estudios recientes sobre la ecologia del forrajeo en las hormigas han enfatizado solamente la relación entre las hormigas y sus recursos alimenticios. Este artículo, aunque en gran parte teórico, sugiere que los predadores de las hormigas, especialmente largartijas y anuros, pueden haber tenido gran importancia en la evolución de la morfología y la ecología del forrajeo de las hormigas. Se usa un modelo teórico simple de

la ecologi̕a del forrajeo en las hormigas para sugerir algunos posibles resultados evolutivos como consequencia de la predación. Datos tomados sobre hormigas abasteciendo en la Isla de Barro Colorado, Panamá, sustentan algunas de estas sugerencias. Sigue una lista de los posibles resultados evolutivos de la predación sobre el forrajeo en las hormigas :

1 – Las especies en las que las hormigas forrajean individualmente y que no tienen buenos métodos de reclutamiento no demuestran polimorfismo entre las obreras. Estas especies pueden resistir a la predación por medio de su tamaño grande, su agresividad, y sus armamentos ; o pueden escaparse por medio de su camuflage, su vida nocturna, o su tamaño pequeño.

2 – Las pequeñas legionarias forrajean escondidas o de noche ; las legionarias más grandes son agresivas y bien armadas. El forrajeo en columnas en estas especies puede estar más relacionado al abastecimiento que a la defensa contra los predadores. El polimorfismo de las obreras en las hormigas guerreras parece estar relacionado a la recolección de recursos.

3 – Los sistemas de defensa basados sobre las alomonas se encuentran generalmente en las hormigas monomorficas, de tamaño pequeño o medio, que frecuentemente tienen el tegumento suave y que forrajean en grupos. Las hormigas que usan alomonas como defensa frecuentemente son manifiestamente pastoras de afidos o recolectoras de nectar.

4 – Las hormigas que generalmente tienen pocas defensas contra los predadores, pero tienen un buen sistema de recolección, pueden emplear una estrategia de reclutamiento de obreras polimórficas.

5 – Las especies en las cuales las obreras mayores pueden desempeñar una función defensiva, pueden tener una estrategia de desplegar obreras polimorficas. El forrajeo en columnas en estas especies puede haber sido seleccionado como un componente importante de esta estrategia.

6 – El forrajeo en columnas también puede encontrarse en especies que solamente en grupos pueden resistir o rechazar a los predadores.

7 – El mimetismo, tanto Batesiano como Mulleriano, parece poder existir entre las hormigas. Con respecto a esto, el hecho que muchas otras familias de insectos y de arañas mimetizan a las hormigas, merece estudio, particularmente con relacion a sistemas de defensa contra predadores de las hormigas que sirven como modelo.

> *«I could never satisfy myself as to the function of these worker-majors. They are not the soldiers or defenders of the working portion of the community, like the armed class in the Termites, or white ants ; for they never fight. The species has no sting, and does not display active resistance when interfered with. I once imagined they exercised a sort of super-intendence over the others ; but this function is entirely unnecessary in a community where all work with a precision and regularity resembling the subordinate parts of a piece of machinery. I came to the conclusion, at last, that they have no very precisely defined function. They cannot,*

> *however, be entirely useless to the community, for the sustenance of an idle class of such bulky individuals would be too heavy a charge for the species to sustain. I think they serve, in some sort, as passive instruments of protection to the real worker. Their enormously large, hard, and indestructible heads may be of use in protecting them against the attacks of insect-ivorous animals. They would be, on this view, a kind of «pieces de resistance», serving as a foil against on-slaughts made on the main body of workers».*
>
> **Henry Walter Bates**
> *The Naturalist On the River Amazons*

Differences in foraging ecology among ant species are widely recognized (see Wheeler, 1910 ; Sudd, 1967 ; Wilson, 1971, and Carroll and Janzen, 1973, for reviews). Most studies of ant foraging ecology have emphasized either the integrative mechanisms of the behavior in a species (Wheeler, 1910 ; Sudd, 1967) or the exploitation of resources by a species or by several competing species (Carroll and Janzen, 1973). The recent general theoretical interest in optimal foraging theory (Pyke et al., 1977) reinforces these perspectives. An overview of these studies would suggest that the investigators' views on ant foraging ecology incorporate the relation between consumers (the ants) and resources as the primary determinants of foraging strategy in the ants themselves (Figure 1). Morphology and behavior in ants are therefore generally interpreted as components of a resource aquisition strategy.

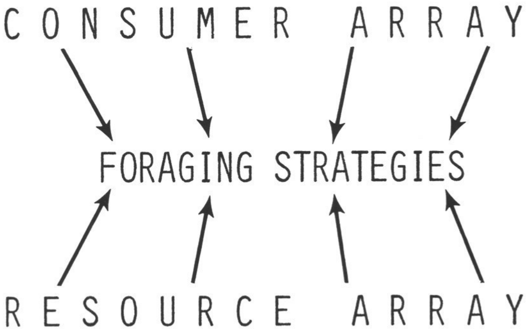

Fig. 1 – Most contemporary studies of ant foraging ecology imply that foraging strategies are the evolutionary result of only two main factors : patterns of resource aquisition and competition among ant species for access to resources.

Fig. 1 – Muchos estudios contemporáneos sobre la ecología del forajeo implican que las estrategias de las hormigas sean el resultado evolutivo de solamente dos factores principales : los patrones de fuentes de abastecimiento y la competencia entre las especies de hormigas para el aceso a los alimentos.

In my own field work with ants in the early 1970's (Hunt, 1977 ; Cody et al., 1977 ; Mares et al., 1977) I noted repeated instances in which it seemed that features of ant foraging strategy, including both behavioral and morphological components, could be interpreted in relation to potential predation by vertebrates that prey upon foraging worker ants. The most notable vertebrates in this regard are lizards and anurans. I did not form the opinion that vertebrate predation is the sole selective force acting on ant foraging strategy ; rather it seemed that an assessment of the potential role played by vertebrate predation could amplify and perhaps clarify an analysis based only on resource considerations. Two examples will clarify my position.

Two species of the formicine genus *Myrmecocystus* (honey pot ants) are abundant at a site I studied in southern California. One, *M. flaviceps*, is exclusively diurnal ; the other, *M. testaceous*, is exclusively nocturnal (Hunt, 1973). The complete separation of foraging times is in marked contrast to the broad overlap in habitats foraged and a probable broad overlap in resources taken. These sympatric congeners thus seem to be a good example of competitors for common resources that have undergone competitive displacement and now occupy disjunct ecological niches (Pianka, 1978). Particular behaviors of each species suggest a further interpretation, however. *M. flaviceps* is active at higher ground surface temperatures (up to 50° C) than any other ant species at the site. By rapidly darting from twig, to pebble, to grass stem, and so on, foragers can cover sites where workers of *Camponotus anthrax*, shaken from their arboreal foraging sites in shrubs, rapidly die from the heat. *M. testaceous*, the nocturnal species, offers a marked contrast. Large numbers of foragers congregate near nest entrances, standing or moving slowly about in a manner never seen in *M. flaviceps*. My interpretation of these behavior differences is that each species has adopted a strategy whereby it can avoid possible predation by the many lizards at the site. *M. testaceous* forages only at a time when the lizards do not ; *M. flaviceps* forages diurnally but over ground surfaces too hot to be traversed by lizards. It seems plausible to me to describe the observed foraging differences as alternative selected responses whereby each species avoids exposure to predation.

A second example involves the well studied New World harvester ants of the genus *Pogonomyrmex*. Hölldobler (1974) detailed the foraging habits of three species in southern Arizona. Two of these, *P. barbatus* and *P. rugosus*, utilize conspicuous trunk trails for foraging, and Hölldobler documented a closer intraspecific spacing of nests for these species than for *P. maricopa*, in which individuals forage without the use of trunk trails. Hölldobler's suggestion that foraging via trunk trails facilitates a finer partitioning of the area foraged than is possible with a more uniform dispersion of individual foragers is most likely correct. Upon inquiry, however, I learned that *P. barbatus* and *P. rugosus* can sting with a potency that is painful but not unbearable, whereas a *P. maricopa* sting borders on excruciating pain (R.R. Snelling, personal communication). I would suggest, then, that studies might reveal that individual *P. maricopa* can successfully repel predators while *P. barbatus* and *P. rugosus* can successfully do so only en masse. The foraging strategies and resource partitioning documented by Hölldobler thus may well reflect alternative strategies of predator resistance.

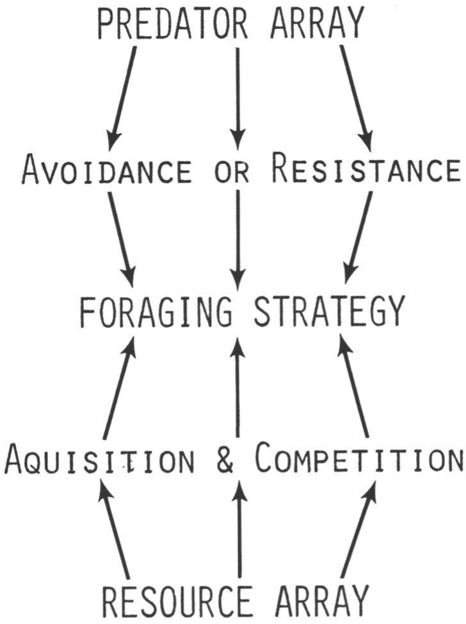

Fig. 2 – It is suggested that ant foraging strategies reflect composite adaptations to several selective pressures. Resource aquisition and competition for resources are, to be sure, important. However, some components of ant foraging strategies, including both morphological and behavioral features, may have been selected for as either avoidance or resistance responses to vertebrate predation.

Fig. 2 – Se ha sugerido que las estrategias de forajeo de las hormigas reflejan adaptaciones a varias presiones selectivas. La recolección de recursos y la competencia para ella son importantes. Sin embargo, algunos componentes de las estrategias del forajeo, incluyendo carácteres morfológicos y comportamentales, pueden haber sido seleccionado para evitar o resistir a la predación de los Vertébrados.

No predation data have been collected on either the *Pogomomyrmex* species studied by Hölldobler or on the *Myrmecocystus* species studied by me, but I feel that do so could both expand the traditional resource based interpretations of the observed foraging strategies and offer insight on the selective mechanism that may have fostered them. I suggest that a complete analysis of ant foraging ecology can be prepared only by simultaneous consideration of both response to predation and access to resources (Figure 2). In the remainder of this paper, then, I propose to speculate on some of the features of ant morphology and behavior that I believe can be interpreted in relation to predator selective pressure. As a first analysis I have prepared a very general classification of ant foraging ecologies that is based only on features of the foraging system itself (Figure 3). Relevant criteria are :

1 – whether workers of a species forage solitarily or in groups ;
2 – for those species that forage solitarily, whether recruitment to resources is lacking, poor, or good ;
3 – for group foraging species, whether the sought for resources are stationary (plants and detritus) or mobile (living arthropods) ; and
4 – for all species, whether the workers themselves are (1) monomorphic, (2) show monophasic allometry, or (3) exhibit complex polymorphism (see Wilson, 1971, for definitions and discussion).

Genera that exemplify various categories have been included in the Figure, and descriptive terms that correspond to each category are given.

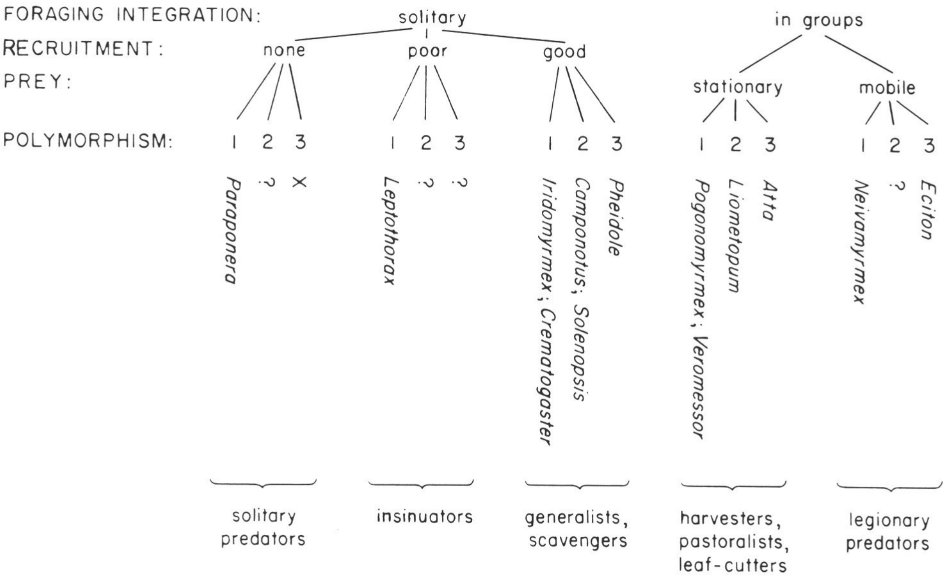

Fig. 3 – A scheme for identifying ecological categories of foraging in ants. The first distinction is whether ants forage solitarily or in groups. For ants that forage solitarily, distinction is made in degree of recruitment : no recruitment, poor recruitment, or good recruitment. For group foraging ants a distinction is made as to whether the sought for resources are stationary or mobile. Polymorphism in all ants is distinguished as 1) monomorphic ; 2) monophasic allometry ; 3) complex polymorphism.

Fig. 3 – Una esquema para la identificación de las categorias ecológicas del forajeo en las hormigas. Se considera primero si las hormigas forajean solas o en grupo. Para las primeras, se distingue el grado de reclutamiento : no reclutamiento, poco reclutamiento o buen reclutamiento. Para las hormigas que forajean en grupo, se distingue si la busqueda de recursos es estática o móbil. Se ha dividido el polimorfismo en todas las hormigas entre : 1) monomórfico ; 2) alometría monofásica ; 3) polimorfismo complejo.

An alternative analysis can be based on criteria that can be presumed to have been selected in response to predation (Figure 4). Two alternatives are available as anti-predator responses : avoidance or resistance. Each strategy dictates particular suites of structural and behavioral traits.

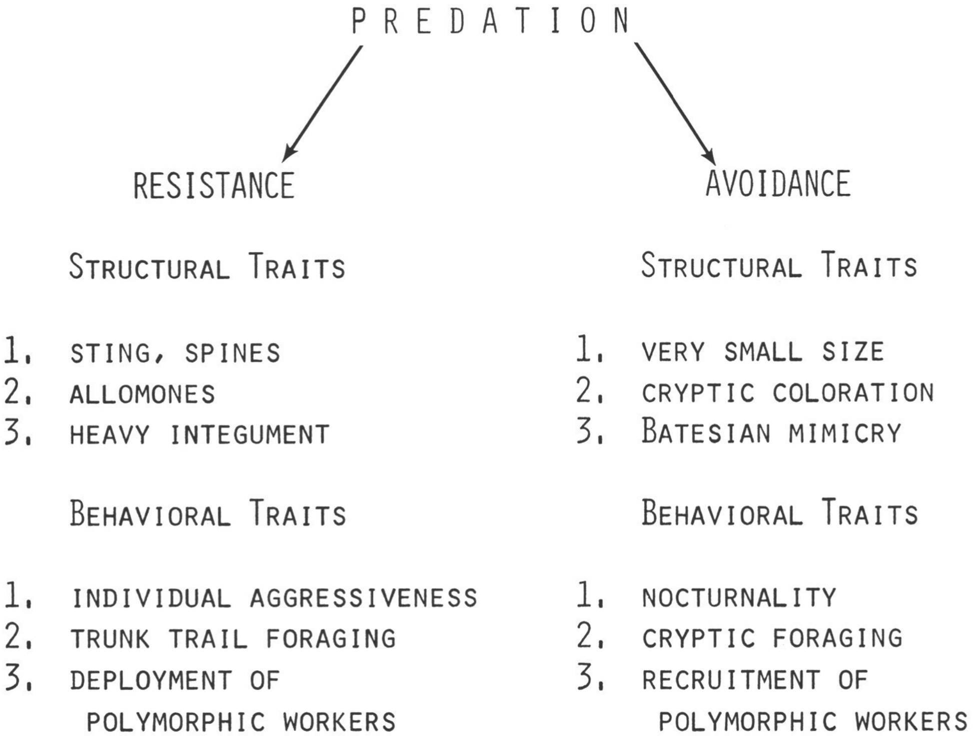

Fig. 4 – Ants subjected to vertebrate predation may have adopted strategies of either resistance or avoidance. Examples of morphological and behavioral traits corresponding to each strategy are listed.

Fig. 4 – Las hormigas expuestas a la predación de los Vertebrados pueden haber adoptado la estrategia de resistir o la de evitar. Estan apuntados ejemplos de carácteres morfológicos o de comportamiento correspondiendo a cada una de las dos entretegias.

By simultaneously considering both of these analyses some speculative propositions can be put forward. The striking absence of worker polymorphism in species that forage solitarily and have poor recruitment or none suggests that such species have few options vis a vis possible predation. One possibility is to resist predation through a combination of individual aggressiveness and a potent sting. Probable examples of this strategy include *Paraponera* in the neotropics, *Pachysma* in Africa, and *Myrmecia* in Australia. An alternative strategy is to avoid predators by cryptive foraging. Species of *Leptothorax* and small ponerine species that recruit via tandem running may exemplify this strategy. Two similar alternative strategies may also apply to legionary predators. Small species of *Neivamyrmex* may avoid predation by foraging cryptively or nocturnally ; larger species such as *Eciton* and *Dorylus* doubtless resist predators by virtue of aggressiveness and potent offensive weaponry. The presence of trunk trail foraging in legionary predators that follow both strategies strongly suggests that such trunk trails are more likely selected for as a resource acquisition strategy than as an anti-predator strategy. The conspicuous worker polymorphism in *Eciton* species seems more closely related to resources rather than to predators.

The largest variety of anti-predator strategies is restricted to two of the foraging ecology groups (Figure 3), solitary foragers with good worker recruitment and group foragers that take stationary resources. Large numbers of ants that are concentrated in a small area, whether by recruitment or by virtue of group foraging, would seem to offer a potentially substantial resource reward to a predator. It seems, then, that anti-predator strategies should be sought in these species even if such strategies are not as immediately apparent as are potent stinging and cryptiveness. One of the more apparent defenses found in these species is the use of repellent or distasteful chemicals. These chemicals, which can be called allomones, are conspicuous in some species. The dolichoderine *Liometopum occidentale* was the most abundant and conspicuous diurnal ant at one of the sites I studied in California (Hunt, 1973). These ants, in groups, produce a pungent aroma that is detectable by humans at distances of a meter or more. Single ants are extremely distasteful to me, and, I suggest, would also be so to any other vertebrate. Less pronounced but similar distastefulness is probably characteristic of most of the subfamily Dolichoderinae. Among myrmicines and formicines, *Crematogaster* and *Formica* exemplify taxa that are capable of exuding or even spraying repellent chemicals such as formic acid. In recent years extensive and excellent work has been done in a number of labs on the biochemistry and physiology of allomone defenses. In the present context, then, I want only to suggest what seem to me to be some foraging strategy correlates of allomone defense systems. These defenses, in my experience, seem limited to ant species that are small to medium in size, that forage in groups, and that lack both stings and worker polymorphism. Most such species seem to specialize on aphid honeydew or on nectar.

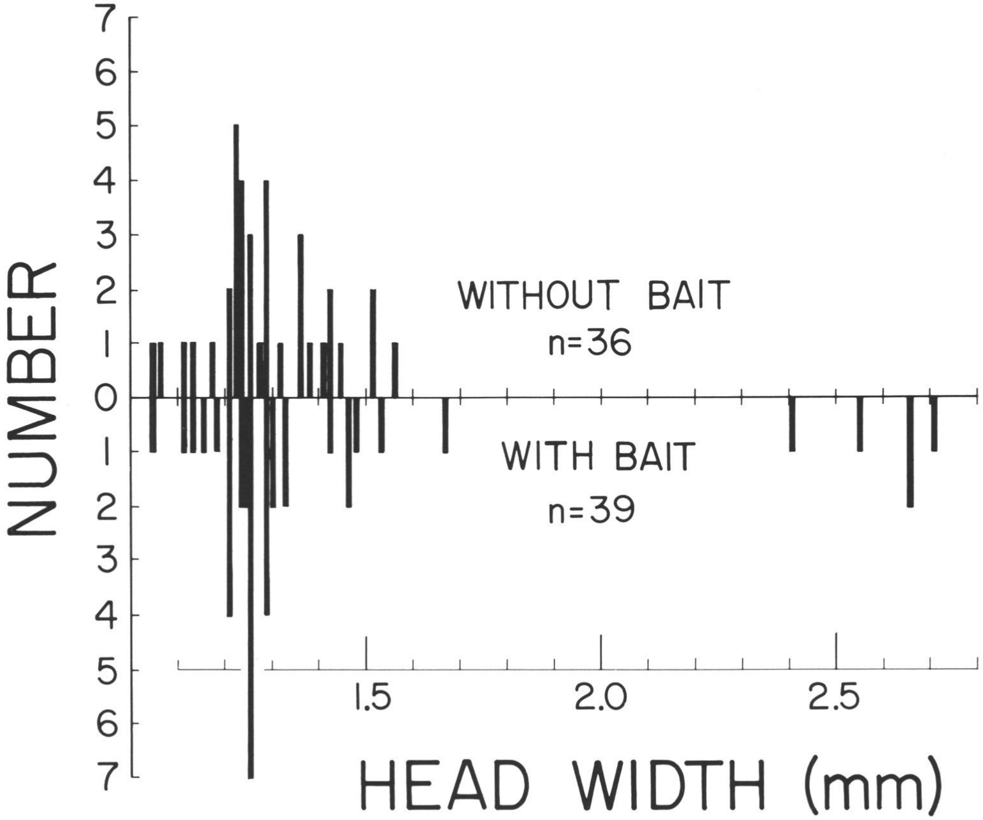

Fig. 5 – Frequency histograms of *Camponotus distinguendus* head widths for workers systematically sampled on two successive days. On the first day, without bait present, no major workers appeared ; on the second day, with bait present, five major workers were taken in the sample.

Fig. 5 – Histógramas de frecuencias de *Camponotus distinguendus* (anchura de la cabeza), siendo las obreras sistemáticamente colectadas durante dos días sucesivos. En el primer día, sin cebo, no aparecieron las obreras mayores ; el día siguente, con cebo, cinco obreras mayores fueron colectadas.

Species that do exhibit worker size polymorphism offer some of the most interesting anti-predator strategies. In Chile I sampled foragers exiting a nest of *Camponotus distinguendus* on two days, one when baits were deployed and one when they were not. Major workers foraged only on the day when baits were present (Figure 5). Carroll and Janzen (1973) cite corresponding results by a number of other investigators, and they suggest that the pattern of foraging by small workers and recruitment of larger workers is in part to minimize the cost per searcher. However, the cost being minimized is not energetic cost of foraging, as reading of Carroll and Janzen might suggest, for equal search areas are doubtless covered with greater energetic efficiency by larger workers. I suggest that the cost being minimized is cost to the colony of loss of a forager to predation. Larger workers that are energetically more expensive to produce are placed at risk only when the probable resource reward merits that risk. I believe that many allometric or polymorphic species in genera such as *Pheidole* and *Camponotus* use this strategy, which I refer to as recruitment of polymorphic workers (Figure 4). This strategy can both optimize resource aquisition and minimize possible loss to predation.

An alternative strategy is employed by *Atta cephalotes. A. cephalotes* is a strongly polymorphic leaf cutter ant that forages using conspicuous trunk trails. The species lacks a sting and is not distasteful, yet it seems to enjoy a puzzling immunity to predation. I suggest that Henry Walter Bates (1892) very nearly correctly assessed the strategy employed when he identified the large major workers as playing a passive defensive role. These large major workers do not cut or transport leaves nor do they work inside the nest. They have, however, sharp mandibles capable of delivering a powerful scissors-like bite (Figure 6). It seems likely to me that a naive predator that ingested such an ant would most likely sustain injury to its mouthparts or gullet. That predator might then well remember the encounter and so avoid any similar future predation attempts. Close-association of the major workers with the foraging workers could then engender an immunity to predation for all. I have referred to this strategy as deployment of polymorphic workers (Figure 4). Other species that deploy major workers, such as *Solenopsis saevissima* (Wilson, 1971), may well be exploiting this strategy.

The trunk trail foraging by *A. cephalotes* may well have been selected for in part, if not primarily, by virtue of its anti-predator value. Working foragers are conspicuously and closely associated with the defensive majors that accompany them. What, then, can be the selective basis for trunk trail foraging in monomorphic species ? The *Pogonomyrmex* species that I discussed at the beginning of this paper include two species that forage using trunk trails. Though a resource based selective mechanism can be argued, I have suggested predation as an alternative. Some anecdotal observations are thus noteworthy. Lizards of the genus *Phrynosoma* are specialist ant eaters that emphasize *Pogonomyrmex* in their diet. R.R. Snelling (personal communication) offered 10 or 12 *Pogonomyrmex californicus* as food to captive *Phrynosoma*, and on two occasions the ants swarmed over the lizards, biting and stinging them. One of the lizards subsequently stopped eating and died of starvation ; the other lizard continued to eat *Formica, Myrmecocystus*, and

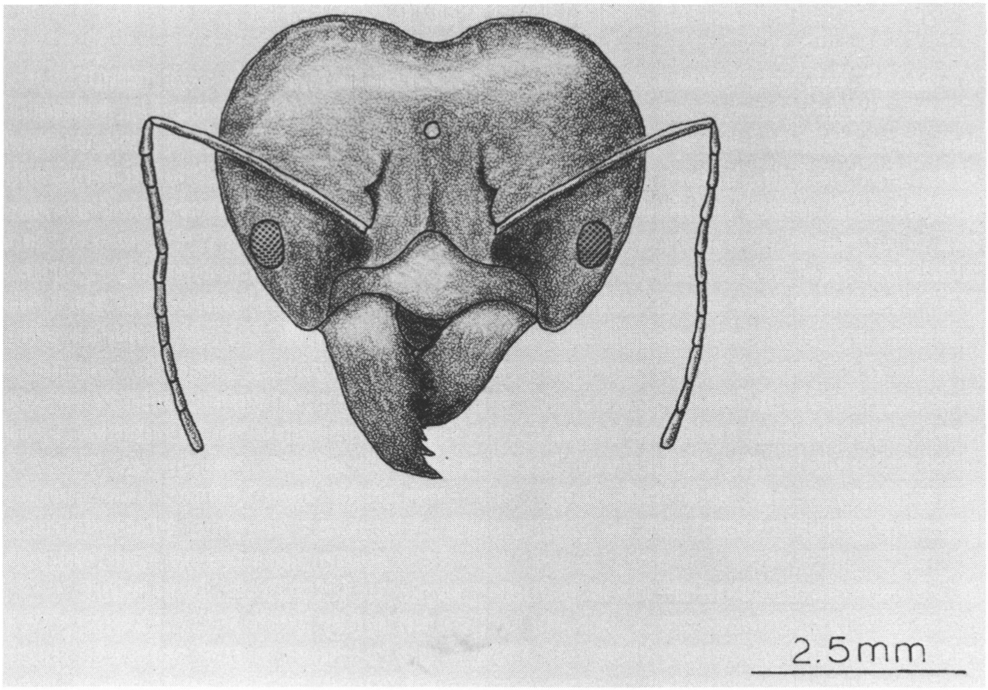

Fig. 6 – An *Atta cephalotes* major worker showing the scissor-like mandibles.

Fig. 6 – Una obrera mayor de *Atta cephalotes* enseñando sus mandíbulas en forma de cizalla.

other ants, but it retreated from all *Pogonomyrmex* and majors (but not smaller workers) of *Solenopsis xyloni*, which somewhat resemble *Pogonomyrmex*. I would expect, then, that *Phrynosoma* in natural situations take primarily isolated foragers of *Pogonomyrmex* either at the sides or terminus of trunk trails. Predation directly upon ants massed in a group could well result in a situation as Snelling observed in captivity. Trunk trail foraging in *Pogonomyrmex* may well have been selected for in those species that can resist predators only en masse. The solitary foraging *P. maricopa* may well be able to resist predators on an individual basis.

At this point I would like to turn to a single brief field study that presents data relevant to my speculations. During February 1-4, 1974, I collected foraging ants at Barro Colorado Island, Panama, in a manner as much like a lizard or anuran as I could conceive. I spent periods of time two hours or longer in the forest each morning, afternoon, and night. I sat motionless for long periods or moved slowly about and collected all foraging ants that I could procure. I made no attemps to disturb leaf litter, displace vegetation, etc. in searching for ants. I simply collected what I saw as I saw it. Sixty-six species were collected in this manner. The ants were collected into 70 % ethanol, and about 3 months later I removed the ants, air dried them on filter paper for five minutes, and then weighed them. The array of ant sizes, by subfamily (Figure 7), shows some noteworthy patterns.

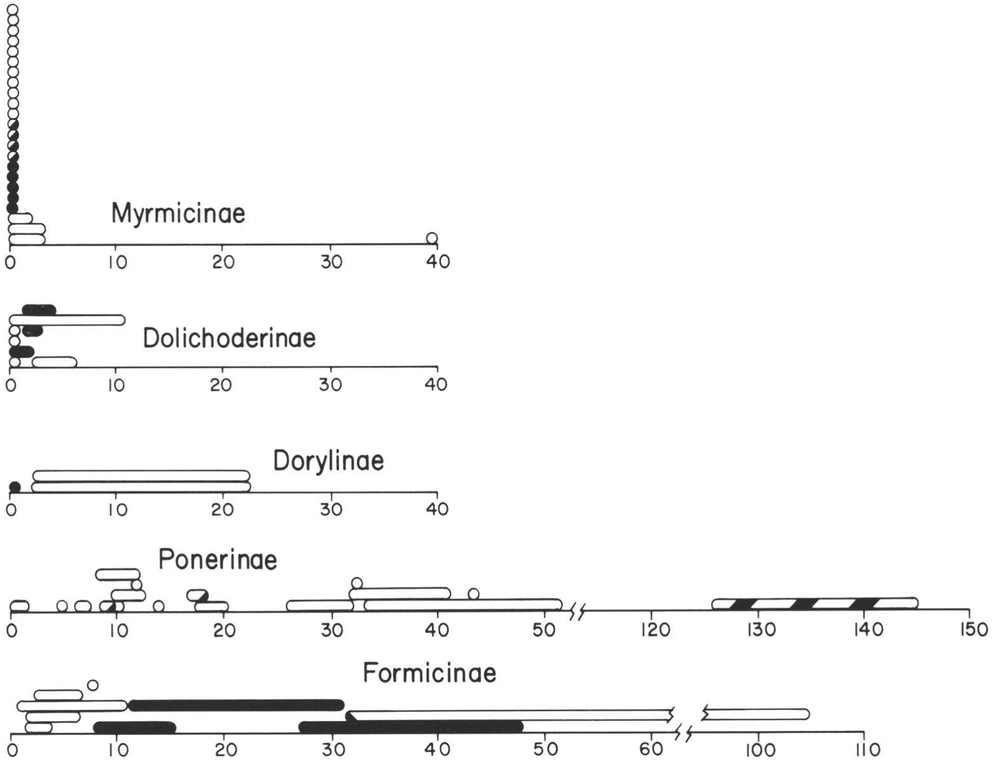

Fig. 7 – Array of weights of worker ants, by subfamily, as collected at Barro Colorado Island, Panama. Ant weights are given on the horizontal axis in milligrams. Each circle or bar represents a single species ; a circle represents either a single specimen or multiple specimens of the same weight ; a bar spans the range of weights for collected individuals of a species. Open figures (o) indicate species collected only by day ; closed figures (●) indicate species collected only at night ; partially shaded figures (o) indicate species collected both day and night.

Fig. 7 – Clasificación, por pesos, de la hormigas obreras colectadas en la isla de Barro Colorado, Panama. Los pesos estan dados en milígramos (eje horizontal), cada círculo o barro representa una sola especie ; un círculo puede representar un solo individuo o varios del mismo peso ; une barra representa la distribución de los pesos en los individuos colectados de una especie. Las figuras en blanco (o) indican las especies colectadas en el día ; la oscruras (●) las colectadas en la noche ; las figuras rayadas (o) indican las especies que se encontraron de día y noche.

All myrmicine foragers but one were small to very small. Many of these species, notably the 11 *Pheidole* species, doubtless have larger workers than were encountered in this sampling. That only small workers were encountered suggests that these ants may employ a recruitment of polymorphic workers strategy and so generally avoid predation. The one large myrmicine encountered, *Cephalotes atratus*, is arboreal, has a very heavy integument, and is conspicuously spinescent (Figure 8) , all of these characters suggest a strategy of resistance to predation.

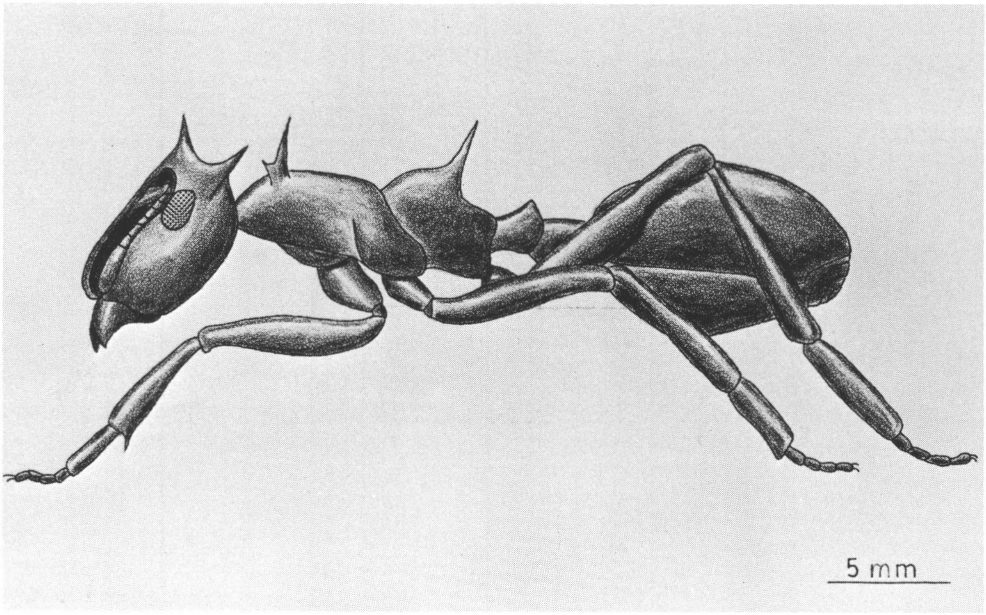

Fig. 8 – A *Cephalotes atratus* forager

Fig. 8 – Una abastecedora de *Cephalotes atratus*

The dolichoderines, which I suggest may be predator resistant by means of allomones, were small to medium in size. Most of the species were found conspicuously foraging in large numbers. The one small doryline encountered was nocturnal. The two *Eciton* species are small to medium sized and are probably resistant to predation by virtue of aggressiveness and sting potency. The ponerine species were medium to large in size, and on three painful occasions in this sampling I was reminded of the potent stinging ability of larger ponerines. The largest species encountered in this sampling, *Paraponera clavata*, is a solitary forager whose sting is held in high regard by all who work in the neotropical lowland forests (Figure 9). *Paraponera* is a conspicuous ant as it forages, and it responds aggressively to attempted capture.

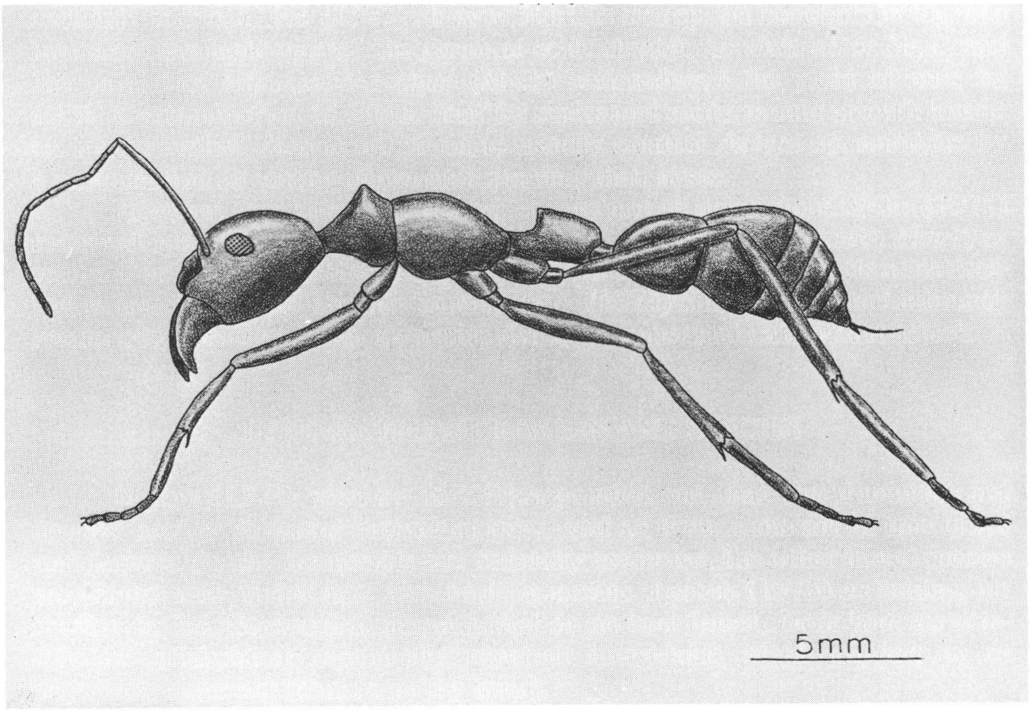

Fig. 9 – A *Paraponera clavata* forager.

Fig. 9 – Una abastecedora de *Paraponera clavata*

The formicines offer some of the most varied patterns. The foragers ranged from small to large. The small diurnal species were largely to exclusively arboreal and so may avoid many predators. The largest species, *Camponotus sericeiventris*, forages both terrestrially and on tree trunks and larger branches, both diurnally and nocturnally. Large workers are seen foraging individually and moving slowly about ; they are characterized by a heavy integument, large head, and powerful mandibles (Figure 10). The other large

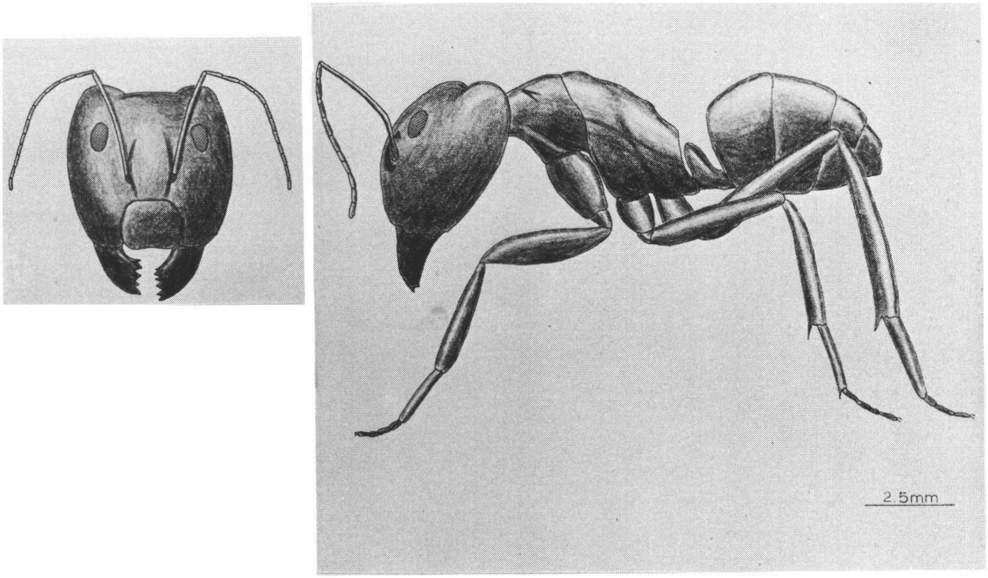

Fig. 10 – A large worker of *Camponotus sericeiventris* collected foraging by day.

Fig. 10 – Una obrera grande de *Camponotus sericeiventris*, colectada forajeando en el día.

formicines are nocturnal. The largest of these, *Camponotus agra*, is typical in having long legs and rapid movement, a soft integument, and a small head with mandibles that are ineffectual in biting (Figure 11). This suite of characters suggests predator avoidance. To me, these patterns in formicinae and those for the other subfamilies all conform to the proposition that is the basis of this paper, that predation by vertebrates has exerted strong selective pressure on morphology and foraging ecology in these ants.

Lastly, let me note that of course there will be exceptions to the generalities I have presented. In some cases, however, these may be the exceptions that prove the rule. Two examples will suffice. In my California studies I noted that species of *Veromessor* harvester ants forage diurnally in conspicuous trunk trails, yet they lack stings, polymorphic workers, and, apparently, allomones. They possess, however, a strong resemblance to *Pogonomyrmex* species. I suggest that they may exploit a mimetic similarity to *Pogonomyrmex*, and I believe, though data are lacking, that they emphasize critical components of the trunk trail strategy : they are more tightly

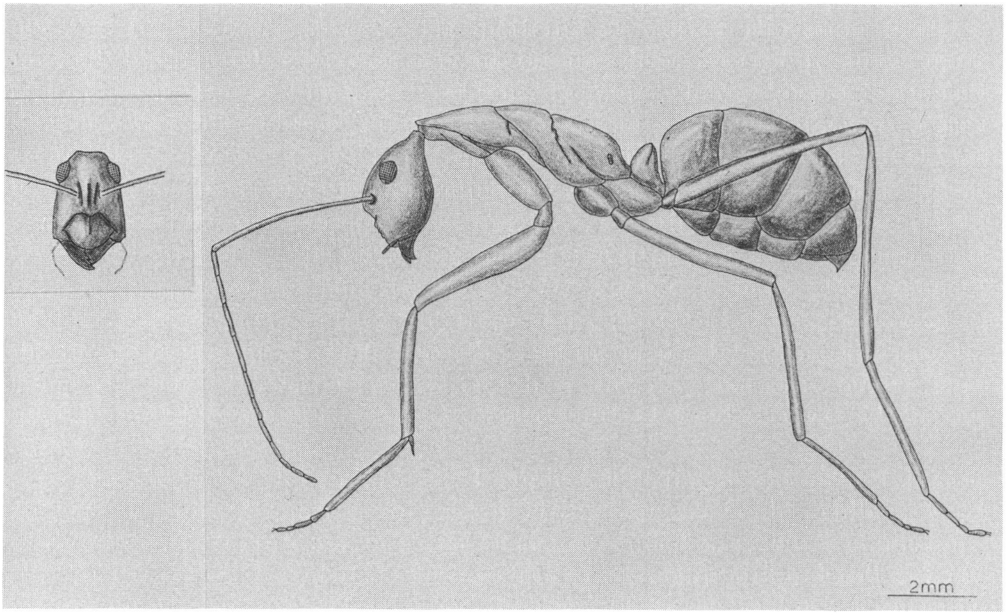

Fig 11 – *Camponotus agra*, a large nocturnal formicine.

Fig. 11 – *Camponotus agra*, una formicina noctuna grande.

massed in the trail and so are generally more conspicuous than are *Pogonomyrmex* ; fewer foragers stray to the sides of the column ; and the foraging fan at the terminus of the column is smaller than in *Pogonomyrmex*. As with all good Batesian mimics, they thus scrupulously minimize the possibility that a predator might discover the ruse. My second exception is from the Amazonian lowlands near Iquitos, Peru. There I chanced upon a diurnal, terrestrial, medium-sized, individual ant that was clearly a formicine. I was immediately struck by this ant as foraging in a manner counter to all my preconceptions based on predation. I watched this ant with great curiosity for several minutes before attempting to collect it, and as I did so I was thoroughly surprised. As I reached for the ant it jumped ! The ant jumped quickly and repeatedly, for distances up to 5 cm, and it successfully evaded capture for a frantic half minute or longer. The species, *Gigantiops destructor*, has the largest eyes in relation to its size of any new world ant known to me (Figure 12). Its unique traits of morphology and behavior seem clearly selected for by vertebrate predation.

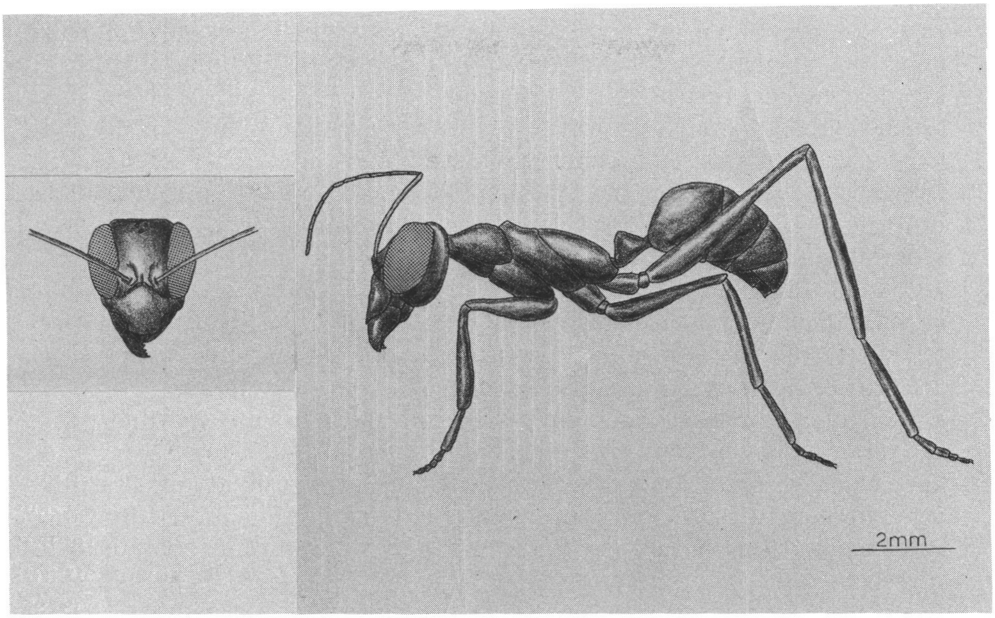

Fig. 12 – *Gigantiops destructor*, a diurnal, terrestrial, solitary foraging formicine from the Amazon lowlands.

Fig. 12 – *Gigantiops destructor*, una formicina de tierras bajas de Amazonas, diurna, terrestre y forajeando sola.

CONCLUSION

In conclusion, I have taken the opportunity provided by this symposium to offer some admittedly speculative ideas on a proposed relation between the foraging and morphology of ants and the role of ant eating vertebrates, notably lizards and anurans, as agents of selection. Many of the ideas I have presented are doubtless not original, and I have probably transgressed on the work of other reserachers. The meagre data I have presented are merely suggestive. I have tried to indicate, however, my conviction that a pattern of varied but coherent responses to vertebrate predation exists in the foraging ecology of ants.

A non-exclusive listing of relevant traits as I see them includes the following :

1 – Species that forage solitarily and have poor recruitment or none also lack worker polymorphism. Such species may either resist predation via large size, aggressiveness, and weaponry ; or they may avoid predation via cryptiveness, nocturnality, or small size.
2 – Small legionary predators forage cryptively or nocturnally ; larger legionary predators are aggressive and have potent weaponry. Trunk trail foraging in these species may be more strongly related to resource aquisition than to predator resistance. Polymorphism in army ant workers seems resource related.
3 – Allomone defense systems are generally found in ants small to medium in size that are monomorphic, that frequently have a soft integument, and that generally forage in groups. Ants with allomone defense systems are frequently conspicuous aphid pastoralists or nectar gatherers.
4 – Ants that are generally defenseless against predators but that have good recruitment may employ a recruitment of polymorphic workers strategy.
5 – Species in which major worker can serve a defensive function may exhibit a deployment of polymorphic workers strategy. Trunk trail foraging in such species may have been selected for as an important component of this strategy.
6 – Trunk trail foraging may also be found in species that can resist or repel predators but only successfully do so when in groups.
7 – Mimicry, both Batesian and Mullerian, seems possible among ants. In this regard the well known ant mimicry among many families of non-ant insects and of spiders seems to call for particular study of the anti-predator defense system of the ant models themselves.

In conclusion, I have tried to indicate in this paper that full consideration of these responses to predation can add perspective and significance to resource centered analyses of foraging strategies in ants. I will close, then, with my personal conviction : when studying the foraging ecology of ants, especially in the tropics, one should assume a major selective role for vertebrates until the data demonstrate otherwise.

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Appendix A : Ants collected at Barro Colorado Island, Panama
February 1-4, 1974

	When collected*	Size (mg)
Subfamily Ponerinae		
Paraponera clavata	ND	128.6-145.9
Ectatomma ruidum	D	8.7-10.1
Ectatomma tuberculatum	N	14.1
Pachycondyla apicalis	D	27.1-32.2
Pachycondyla carinulata	D	6.3
Pachycondyla harpax	D	10.3-12.0
Pachycondyla impressa	D	34.4-52.2
Pachycondyla laevigata	D	12.0
Pachycondyla obscuricornis	D	17.0-19.4
Pachycondyla striatiodis	D	8.8-11.4
Pachycondyla velosa	D	45.1
Anochetus inermis	D	1.1
Odontomachus chelifer	ND	33.3-41.0
Odontomachus haematodus	ND	16.3-17.4
Odontomachus minutus	N	4.2-4.8
Subfamily Dorylinae		
Eciton burchelli	D	1.8-25.0
Eciton hamatum	D	2.3-23.8
Neivamyrmex sp.	N	0.3-1.0
Subfamily Pseudomyrmecinae		
Pseudomyrmex sp. A	D	2.0-2.5
Pseudomyrmex sp. B	D	0.9
Subfamily Myrmicinae		
Aphaenogaster sp.	D	0.9
Pheidole sp. A	D	0.1-0.3
Pheidole sp. B	D	0.3

*N : night – D : day

	When collected	Size (mg)
Pheidole sp. C	N	0.2
Pheidole sp. E	N	0.3
Pheidole sp. F	D	0.1
Pheidole sp. G	N	0.3
Pheidole sp. H	D	0.3
Pheidole sp. I	D	0.3
Pheidole sp. J	N	0.3
Pheidole sp. K	ND	0.1-0.4
Pheidole sp. L	ND	0.2-0.3
Crematogaster sp. A	D	0.3
Crematogaster sp. B	N	0.4
Solenopsis sp. A	D	0.2
Solenopsis sp. B	D	0.2
Ochetomyrmex auropunctata	ND	0.1-0.3
Cephalotes atratus	D	39.3
Paracryptocerus multispinosus	D	0.4-0.9
Sericomyrmex amabilis	D	0.7-0.9
Apterostigma mayri	D	0.6
Cyphomyrmex rimosus	ND	0.3
Cyphomyrmex salvini	D	0.9
Trachymyrmex morgani	D	0.8-1.2
Trachymyrmex sp. A	N	2.8
Trachymyrmex sp. B	D	0.9
Trachymyrmex sp. C	D	2.0
Subfamily Dolichoderinae		
Dolichoderus laminatus	ND	2.4-5.0
Azteca sp. A	N	0.7-1.3
Azteca sp. B	D	0.4-0.9
Azteca sp. C	D	0.3
Azteca sp. D	N	0.6
Azteca sp. E	N	1.2-2.4
Azteca sp. E	D	0.3-10.9
Azteca sp. G	N	1.0-3.4
Subfamily Formicinae		
Camponotus abdominalis	N	7.7-14.5

	When collected	Size (mg)
Camponotus agra	N	27.0-47.0
Camponotus brettesi	D	1.0-2.0
Camponotus brevis	D	1.1-5.4
Camponotus lindigi	D	0.3-10.9
Camponotus sericeiventris	ND	31.1-105.5
Camponotus simillimus	N	11.0-29.5
Camponotus zoc	D	2.3-5.6
Dendromyrmex chartifex	N	7.3