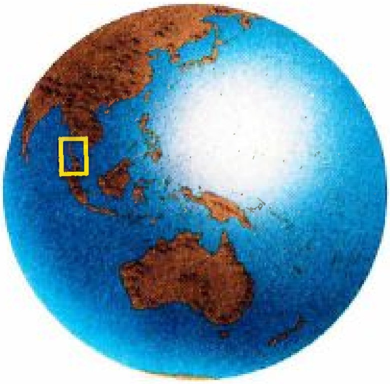
Mark W. Moffett

Cooperative Food Transport by an Asiatic Ant



Pheidologeton diversus is perhaps the most proficient of all group-transporting species. Workers carry objects as much as 5000 times their weight and 10 000 times their volume in groups of as many as 100 ants. Workers in groups carry more weight per ant than do solitary workers, and the efficiency of group transport (defined for the purposes of this report as [burden weight times velocity] divided by number of carriers) increases with increasing burden size up to a limit, and then declines. The decline is probably a result of the limited availability of space around the perimeter of heavy burdens for ants to grasp. Some possible advantages of group transport are considered for ants.

Group transport is the conveyance of a burden by two or more individuals (Moffett 1987a). (A similar term, "group retrieval," has usually been applied when ants retrieve food along a common path, regardless of the occurrence of group transport.) Group transport has seldom been recognized as a form of social behavior that is worthy of investigation in its own right. Indeed, while group transport is virtually unique to ants (Moffett 1987a), many recent reviews of ant foraging strategies ignore group transport (e.g., Carroll & Janzen 1973, Oster & Wilson 1978, Sudd 1982). With respect to burden size and the numbers of ants that can join forces, group transport is best developed in *Pheidologeton* (Figure 1) (Moffett 1987b, in press a) and *Oecophylla* (Hölldobler 1983) (Figure 2), perhaps followed most closely by certain army ants (Franks 1986, Schneirla 1971) and *Novomessor* (Hölldobler et al. 1978).

The author's observations in 12 Asian countries indicate that all species of the myrmicine genus *Pheidologeton* are probably proficient at group transport. This paper examines the effectiveness of group transport of food in perhaps the most dedicated of all group-transporting species, *Pheidologeton diversus:* workers can group-transport food, brood (in emigrations), refuse (to middens), building material such as soil (for making arcades over trails), and even fellow workers and queens (Moffett in press b).

Like army ants (Dorylinae and Ecitoninae), *P. diversus* ants search for food in groups ("raids") (Moffett 1984). Previous research on *Pheidologeton* ants has focused on their raiding patterns and division of labor (Moffett 1987b, in press c). Three worker subcastes (minors, medias, and majors) can be distinguished on the basis of the workers' size. Workers advance in narrow column raids or fan-shaped swarm raids; food is taken during raid advance. Foods are retrieved primarily by minor workers, but sometimes medias assist minors or carry food in-

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dependently. In addition, minors commonly ride on top of the food.

Is group transport an efficient means of food retrieval? Ideally this question could be answered through laboratory studies of foraging energetics. Unfortunately, captive *Pheidologeton* fail to show normal transport behavior, so group transport had to be studied under field conditions. The results show that group transport is an effective means of retrieving many foods rapidly using a minimal labor force.

Methods

To document food transport in undisturbed situations, 50 to 300 burdens were collected from the trails of 34 *P. diversus* colonies from India, Singapore, Malaysia, Thailand, Indonesia, and the Philippines. Exceptionally large and unusual burdens were collected at other times for measurement and identification. Certain aspects of the transport process were clarified by photographs taken at magnifications of ×2 to ×10.

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Figure 1. Pheidologeton diversus *minor workers carrying a centipede.*

Quantitative studies were made on *P. diversus* colony number 65-82 from Singapore (Moffett 1987b), using partially crushed "Grainut Cereal" (Sanitarium Health Foods, Sydney, Australia). The cereal consists of masses of variable size (i.e., <0.01 mg to >0.3 g) composed primarily of whole-meal flour. This food was chosen because of its apparent uniform density and the fact that burdens did not fragment easily during analysis. The broad range of burden sizes the ants could choose from assured that a variety of group sizes would be required for transport.

A 10-cm-diameter area near the main trunk trail of colony 65-82 was covered with the cereal, and a column of ants was guided there by laying a seed trail to the site. Observations were made along the path taken by the ants at a point 20 cm from the pile of cereal. For each observation the first burden to pass this point that was carried by a previously chosen number of ants was selected. Recorded were: the number of ants lifting the burden, the number riding on the burden, the time taken to carry the burden 20 cm, and the burden's weight (determined to the nearest 0.01 mg after collecting each burden). Burdens were rejected if their paths were obstructed even temporarily, or if they ceased moving for any reason for two seconds or more. Also discounted were burdens that gained or lost ants during the timed interval. Medias participated in transport too seldom to obtain a useful sample size; only burdens carried by minors are considered here.

The experiments were conducted during a week of dry weather every day between 0700 and 0900 hours. Extended intervals of data collection were avoided because the cereal absorbed moisture when kept outside for long periods. Between experiments and before weighing, the cereal was kept in an airtight container with a desiccant. On the sixth day of study the ants began to respond more feebly to the cereal, and on the seventh day little food was taken (similar declining responses occurred toward other foods provided day after day to a given colony; Moffett 1987b). These days were therefore excluded from the analysis, limiting the data to 260 burdens collected during the first five days.

Results

Behavior of Ants Transporting Burdens

Ants gathered around food items at the site of their discovery, gnawing on them and pulling. Often an item was at first moved about slowly in shifting directions. Ten minutes or more were sometimes needed for the ants to sort out their actions so that transport could begin. This was particularly true when numerous items were available, as in the cereal experiments; isolated objects were usually removed within minutes.

Detailed studies, like those of Sudd (1960, 1965), were not made on movement patterns of transporting ants. However, certain aspects of transport behavior were clear from examination of about 600 photographs of this activity. Workers carry burdens rather than drag them. This was apparent from the narrow gap usually visible between the burden and the ground in lateral view. Ants carrying burdens solitarily grasped them between their mandibles, lifting the burdens from the ground and holding the burdens ahead of them as they walked forward (burdens were rarely slung beneath the body). Group-transporting ants carried burdens differently. One or both forelegs were placed on the burden, and appeared to aid considerably in lifting it. The mandibles were open and usually lay against the burden, but the burden's surface was seldom gripped between them. Burdens small enough to be carried by few ants, as well as small appendages extending from larger burdens, were often carried partly by ants that behaved as described for those engaged in solitary transport.

Workers in groups showed different movement patterns corresponding to their positions around the perimeter of a burden with reference to the direction of transport. Workers at the forward margin walked backward, pulling the burden; those along the trailing margin walked forward, apparently pushing it. The ants along the sides of the burden shuffled their legs more or less sideways, and usually slanted their bodies in the direction of transport (Figure 1; Moffett 1986:280–281).

Transport often ceased when burdened ants encountered impediments. Often in such cases only a few seconds were needed to reestablish progress after removal of the impediment. Typically the ants maintained their grip on the object during the interruption, and afterward carried the burden with the same edge directed ahead. Thus the leg movement patterns of the various ants around the burden perimeter usually remained basically unchanged throughout the period of transport.

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Figure **2. *Top,*** Eciton hamatum *carrying a polybiine wasp pupa.* ***Center,*** Oecophylla smaragdina *carrying a bee.* ***Bottom,*** *African driver ants of the genus* Dorylus *transporting prey. The long-legged workers grasp prey items with their mandibles and straddle the items which then project backward beneath their bodies.*

William H. Gotwald Jr.

Medias composed 1 to 2% of burden-carrying ants. Large burdens (i.e., those hoisted by 25 ants or more) were often carried in part by one or more medias, but even here medias rarely accounted for 5% of carriers. Medias were not required to transport even the largest burdens, as transport continued in cases where they were removed. They were most common at the forward or trailing ends of burdens.

Characteristics of Food Burdens in Undisturbed Colonies

Items markedly smaller than a minor worker were taken by single minors, while most bulkier foods were carried by groups. The percentage of food items carried by groups varied depending on the specific foods being collected (Moffett 1987b). Group-transported foods included both animal material (usually prey) and plant matter (notably seeds). However, many soft or moist foods (rotten fruit, for example) were either apportioned into pieces portable by single ants, or transported in worker crops after being ingested by the ants on the spot.

Among the bulkiest burdens recorded was a 0.60-g spheroidal seed, carried vertically down a tree trunk by a group of about 50 minor workers. The seed had a volume equivalent to about 9600 minors, as measured by water displacement.

A 10-cm earthworm was one of the heaviest burdens recorded, weighing 1.92 g (dry weight 0.55 g) or >5000 times as much as a single 0.30- to 0.40-mg minor worker. This worm was borne by about 100 ants (including eight medias) which transported it at 0.41 cm/s on level ground. In contrast, as ants carried food solitarily on the same trail they moved at 1.03 ± 0.42 cm/s ($\bar{x} \pm$ SD; range 0.37 to 1.94 [$n = 30$]), and their burdens were at most about five times their body weight (unburdened ants moved at 1.62 ± 0.21 cm/s [$n = 30$]). Thus the ants that carried the worm each held at least 10 times more weight than did solitary workers, with only a modest loss in velocity.

Experiments on Group Transport

The results of the experiments with cereal are presented in Figure 3. The velocity of burden transport declined for burdens that required more carriers, at least for extreme group sizes. Concurrently, the weight under transport increased rapidly with increasing number of carrier ants; the relationship between the number of carriers (N) and burden weight (W) can be described by $W = 26.64 \times N^{2.044}$ ($r = 0.9001$). The weight per ant also increased with the number of carriers. For example, ants carrying the largest burden recorded during this experiment each held $\times 4.30$ the weight of the heaviest burden recorded for a single ant. The value obtained by multiplying burden weight and velocity—which can be taken as an index of transport efficiency if carriers are in unlimited supply—increased with group size at least up to groups of eight to 10 ants. The transport efficiency per ant also increased with group size (or burden weight) to a maximum for groups of eight to 10 ants, and then declined (difference in efficiency between group sizes eight to 10 and 11+ is significant [$p < 0.001$, Student's t test]).

Although the ants riding on top of food did not aid in transport, their probable defensive role (Moffett 1987b) suggests that their presence could represent a part of transport costs. The results discussed above are similar when riders are included as part of the transporting population. However, the transport efficiency of groups of 11+ ants was in this case not significantly lower than for groups of eight to 10 ants ($p > 0.05$).

The number of workers that might transport an object is limited by the space available around the circumference of that object. Since burden weight is proportional to burden volume (given uniform density), the circumference of a burden is proportional to the cubed root of the burden's weight for spherical burdens. Most cereal burdens were more or less globular, and the cubed root of their weight was therefore used as an approximation of the perimeter available to the ants. The results show that workers tend to become more packed around burdens as the burden size increases, up to a limit (Figure 4). Photographs suggest that most ants around large burdens are just close enough together to permit movement without treading on each other.

Discussion: a Review of Group Transport in Ants

In ants and certain other social animals, food is often eaten in the confines of a nest or other protected site. Since most foods must be torn apart at some point before consumption, the difference between handling food by group transport and carrying small pieces of dissected food solitarily can be considered basically in terms of the merits of tearing apart food before or after retrieval to this site. Generally the fastest method of retrieval maximizes the rate of food intake and reduces interference from competitors outside the nest that could preempt the food.

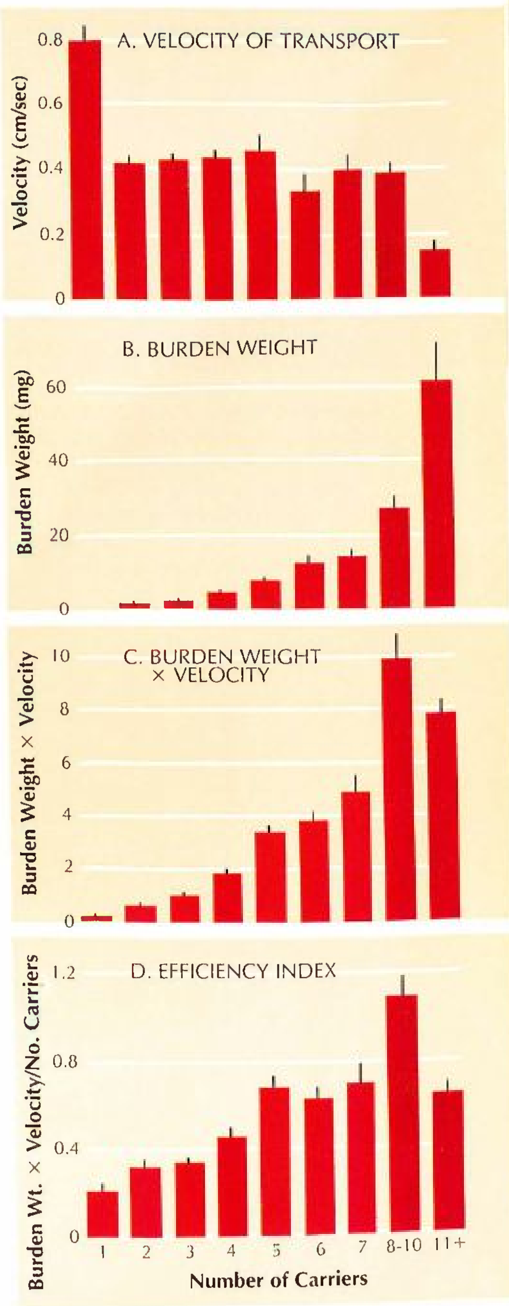
In group transport *P. diversus* can carry for any specified distance far more weight per individual per unit time than solitary ants (Figure 3D). However, a complete assessment of the effectiveness of the group-transport strategy in this species must include the time lost before group transport begins, while ants accumulate at the food and sort out their activities until a coordinated pattern of movement emerges. Although a detailed analysis of this "handling time" was not carried out, the time loss for cereal burdens and many other foods appears to be negligible when compared with the time needed to dismantle the same food on the spot. For example, a large piece of immobilized cereal was removed in pieces over a period of 70 minutes, while neighboring, dislodgeable pieces of similar size were carried off within five minutes. This leaves no doubt that group transport can be a very efficient means of retrieving food.

Group transport is likewise a highly effective means of food retrieval in at least some other ants, for example *Novomessor cockerelli* (Hölldobler et al. 1978) and *Eciton burchelli* (Franks 1986).

The behavior is probably still economical in species with less coordinated group transport, since, despite the slowness of retrieval, dealing with many foods in any other way is even more time-consuming. The difficulty such species must overcome is the antagonism among workers that pull the food in conflicting directions. As Sudd (1960, 1965) demonstrated, this antagonism can be so strong that workers on occasion completely fail to move their prey. *P. diversus* workers are comparatively quick to sort out their activities, so that ants at each point around the burden walk with an appropriate pattern with reference to the direction of transport. The methods used by workers in choosing their leg movements and in sorting out which part of the burden is directed forward are yet to be investigated.

In contrast, the species *Pheidologeton pygmaeus* is unsuccessful at moving food in groups. (*P. pygmaeus* actually should not be considered a *Pheidologeton,* although it is closely related to that genus [Moffett 1987a].) Instead, ants tear even small prey into tiny chunks for individual transport. A worker carrying a larger item is brought to a standstill when others on the trail try to grasp its burden. Transport only begins af-

Figure 3. Experimental data for Pheidologeton diversus *ants carrying cereal burdens in groups of different sizes, including* **(A)** *the velocity of transport,* **(B)** *burden weight,* **(C)** *burden weight multiplied by velocity, and* **(D)** *the efficiency index [(burden weight × velocity)/number of carriers]. Black lines above the bars indicate one standard error. Sample sizes for each number of carrier ants: one,* n = *50; two,* n = *25; three,* n = *47; four,* n = *42; five,* n = *38; six,* n = *16; seven,* n = *20; eight to 10,* n = *12; 11 +,* n = *10.*



ter the other ants let go, or after the burden has been torn into smaller pieces. Because of this, even small insect prey take considerable time to retrieve to the nest (Moffett 1987a).

Burden Size and Shape

Judging from data on *P. diversus* and other ants (Moffett 1987a), group transport is most effective with dry to slightly moist foods of discrete sizes within the range the ants can handle. Most other foods are better dealt with by other means. Soft or moist foods like rotten fruit are comparatively difficult to transport in groups, but easy to harvest on the spot. *P. diversus* usually tear such foods into tiny pieces, or consume the food where it lies. Foods that can be ingested directly may be especially desirable, since the mandibles of laden ants remain unburdened, permitting workers to perform other tasks before returning to the nest. *P. diversus* workers that participate in many exterior tasks are more often replete than those leaving the nest (Moffett 1987b); apparently some ants continue to work after ingesting moist foods.

With foods potentially subject to group transport, the space available for carriers to grasp could in part determine how burdens are handled. As burden weight increases for foods of a given shape and density, the perimeter increases, but more slowly. This probably often limits the burden size that can be transported, since at some point not enough carriers are accommodated by the perimeter to move the food. This could explain the decline in efficiency observed for large cereal burdens in *P. diversus* (Figure 3D). The ants never took cereal burdens much larger than 0.10 g, even though cereal fragments as heavy as 0.30 g were available. Transport of heavier burdens would presumably be possible if the cereal were less dense or if the burdens had a greater perimeter (e.g., were more elongate).

Thus the heaviest burdens carried by *P. diversus* (i.e., those between 1 and 2 g) were of low density (often prey corpses) and were almost always elongated (like worms or centipedes). Elongated burdens were also less likely to become entangled in obstructions near a trail. Similar booty of even larger size was not readily transported, and instead was torn apart in situ. Such observations indicate that different foods show different relationships between transport efficiency and group size, depending on weight, density, and shape. Thus the transport efficiency for earthworms would be expected to begin to decline only for much larger groups (and burden weights) than for cereal burdens (Figure 3D).

The largest booty carried by driver ants is also elongated (Gotwald 1974), but here the method of transport (straddling prey, as in other army ants [Schneirla 1971]) presumably sharply limits both burden shape and the potential number of porters.

Group Transport Is Apparently More Efficient

A hypothesis worth pursuit is: among ants group transport uses the available labor force better. Consider several ways this might prove true:

(1) The number of workers needed to dissect food within a certain time period is probably the same regardless of the food's location. Yet if food is torn into pieces where it is found, the time and energy required to recruit the necessary work force to the food site could represent an additional cost to the colony.

(2) Food retrieval by group transport requires fewer workers. This is certainly true of *Pheidologeton*, and is probably the case for other ants (e.g., Franks 1986). For example, the largest piece of cereal recorded during the experiments was carried by 14 ants. If the ants had first

gnawed that burden into chunks the size of the average cereal burden carried by ants working alone, 498 ants would have been needed to retrieve the same food.

(3) Group-transporting species possibly take greater advantage of the often large pool of workers available within nests, which usually includes workers that do not forage. If such workers aid in dissecting food after retrieval, more of the forager population could conceivably be freed for other activities.

(4) When food is torn up at the site of discovery, the food remains outside the nest longer than it would if transported to the nest entire (unless group transport is very inefficient). Thus any defensive contingent of ants connected with this food must be employed over a longer period. In some ants, a caste serving primarily for defense is common along recruitment trails and at food sites (Wilson 1971). Even in species lacking a specialized defensive caste, defense may entail recruitment of an excess work force at the food site. In many species, more workers often accumulate at food than can possibly harvest the food. In *P. diversus* these excess ants serve at least in part for defense, since they can drive away competing species.

This suggests that defense costs could often be lower for group-transporting species. The opposite may be true if competitors respond preferentially to large, mobile burdens. *Bengalia* flies steal food transported by *P. diversus* workers (Jacobson 1910, Moffett 1987b), and the author's observations suggest that they prefer items carried by small worker groups over those transported by single ants. Workers riding on top of burdens can defend them from *Bengalia* attacks (Moffett 1987b).

(5) Another advantage of group transport in ants is that once the food is inside the nest, the often time-consuming process of tearing it apart can be delayed at the colony's convenience, for example, until periods when foraging has slackened or ceased. In extreme cases some foods (notably seeds) could conceivably be stored in the nest for extended periods, whereas if the same food had been dissected for transport, long-term storage would have been impossible. Harvesting ants, such as some *Pheidole*, store seeds in the nest (Wilson 1971), but it is unclear whether these reserves can include seeds that could only have been procured by group transport. *P. diversus* ants probably quickly consume all food.

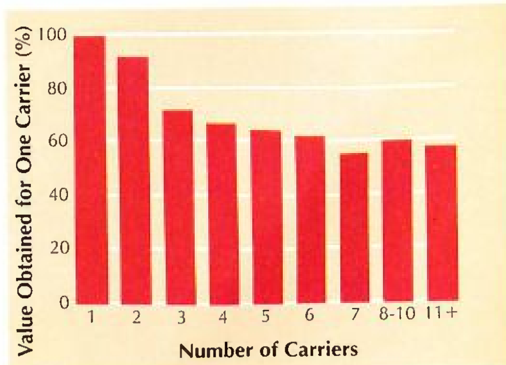


Figure 4. Approximate circumference of burden available per ant, calculated as the cubed root of mean burden weight for each group size, divided into the number of carriers (see text).

Media Workers Versus Minor Workers

A question worthy of study in *Pheidologeton* is the efficiency of media workers at carrying food compared with minor workers. (This study focused on burdens carried only by minors, which vary little in size.) Medias are expected to expend less energy than minors in carrying burdens, because the net cost of transport declines with increasing size in ants (Nielsen et al. 1982). Also *P. diversus* medias clearly can carry more weight than minors. Nonetheless, the medias participated in food transport no more often than expected based on their frequency among foragers, which is $<2\%$ (Moffett 1987b). Medias of the related species *P. silenus* have not been observed to carry food (Moffett in press a). The rarity of medias in food transport could be a solution to an ergonomic problem of optimizing caste ratios and allocating the time–energy budgets of the castes to various tasks. Medias perform several tasks outside the nest (Moffett 1987b, in press a).

Energetics

The experiments on *P. diversus* show that the rate of food intake per ant is higher for workers involved in group transport than for those carrying food alone. Whether group transport yields a net energy savings is yet to be determined, since the difference in energy load to the ants is unknown. Studies on the energetics of the group transport process will require species that show normal transport behavior in captivity, which *Pheidologeton,* in the author's experience, do not.

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Bibliography

Carroll, C. R.; & Janzen, D. H.

1973. Ecology of foraging by ants. *Annual Review of Ecology and Systematics* 4:231–258.

Franks, N. R.

1986. Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli,* Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 18: 425–429.

Gotwald, W. H. Jr.

1974. Predatory behavior and food preferences of driver ants in selected African habitats. *Annals of the Entomological Society of America* 67:877–886.

Hölldobler, B.

1983. Territorial behavior in the green tree ant *(Oecophylla smaragdina). Biotropica* 14:241–250.

Hölldobler, B.; Stanton, R. C.; & Markl, H.

1978. Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera): chemical signals. *Behavioral Ecology and Sociobiology* 4:163–181.

Jacobson, E.

1910. *Pheidologeton diversus* Jerdon und eine myrmecophile Fliegennart. *Tijdschrift voor Entomologie* 53:328–335.

Moffett, M. W.

1984. Swarm raiding in a myrmicine ant. *Naturwissenschaften* 71:588–590.

1986. Marauders of the jungle floor. *National Geographic* 170:272–286.

1987a. Sociobiology of the ants of the genus *Pheidologeton.* Ph.D. thesis, Harvard University.

1987b. Division of labor and diet in the extremely polymorphic ant *Pheidologeton diversus. National Geographic Research* 3:282–304.

In press a. Foraging behavior in the Malayan swarm-raiding ant *Pheidologeton silenus* (Hymenoptera: Formicidae: Myrmicinae). *Annals of the Entomological Society of America.*

In press b. Nesting and emigrations in two group-hunting myrmicine ants (Hymenoptera: Formicidae: *Pheidologeton*). Arnett, R. H., editor: *Advances in Myrmecology.* E. J. Brill, Leiden, Holland.

In press c. Foraging dynamics in the group-hunting myrmicine ant *Pheidologeton diversus. Journal of Insect Behavior.*

Nielsen, M. G.; Jensen, T. F.; & Holm-Jensen, I.

1982. Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* L. (Formicidae). *Oikos* 39:137–142.

Oster, G. C.; & Wilson, E. O.

1978. *Caste and Ecology in the Social Insects.* Princeton University, Princeton, N.J.

Schneirla, T. C.

1971. *Army Ants: a Study in Social Organization.* Freeman, San Francisco.

Sudd, J. H.

1960. The transport of prey by an ant, *Pheidole crassinoda* Emery. *Behaviour* 16:295–308.

1965. The transport of prey by ants. *Behaviour* 25:234–271.

1982. Ants: foraging, nesting, brood behavior and polyethism. Hermann, H. R., editor: *Social Insects,* vol. 4. Academic Press, New York, 107–155.

Wilson, E. O.

1971. *The Insect Societies.* Belknap Press of Harvard University, Cambridge, Mass.

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