Ant Foraging

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Cooperative Foraging in *Daceton*, with a Survey of Group Transport in Ants

Unlike the solitary predation typical of other species of the ant tribe Dacetini, Daceton armigerum *shows cooperative foraging behavior, with stable foraging routes, recruitment to food, and rudimentary group transport of large booty. Carriage of brood by* Daceton *worker groups is much better coordinated than carriage of food. In contrast, most ant species are totally incapable of group transport of food; the minority that show it, like* Daceton, *tend to have large colonies and well-developed mass recruitment behavior and to eat food of discrete sizes, such as insects or seeds. Group transport of bulky larvae and pupae is probably nearly universal in ants and is likely to have preceded the transport of food by this method. More care must be taken in recording the presence or absence of group transport in studies of ant behavior.*

ONE OF THE MOST STRIKING New World ant genera is *Daceton*, with a single known species, *D. armigerum*. Queens and workers have spiny bodies and remarkable lobed heads that can be pivoted back for trophallaxis (regurgitation between individuals). Unlike the simple social organizations typical of most members of the tribe Dacetini (e.g., in *Acanthognathus*[30]), *Daceton* colonies (Figure 1) are large, with workers showing cooperative foraging behavior such as group transport of prey and marked physical polyethism (division of labor based on worker size[37]).

The growth relationships of worker body parts and the worker size-frequency distribution indicate that *Daceton* lacks morphologically definable worker subcastes.[31] Nevertheless, the polymorphism of *Daceton* workers is dramatic.

Widespread in the moist tropical forests of South America, *Daceton* ants are very seldom seen because they are arboreal. Almost all of what we know of this species comes from E. O. Wilson,[37] who observed them in the field, and from B. Hölldobler, J. Palmer, and M. W. Moffett,[19] who investigated recruitment in the laboratory. This paper focuses on cooperative foraging behavior in nature that is not covered in detail elsewhere: recruitment trails and group transport in this species.

Group transport (the carrying or dragging of a burden by two or more individuals[29]) is better developed in ants than in any other animal group. Included in the discussion is a survey of group transport in ants.

Methods

The study colony was collected on 6 May 1988 in an area of lowland rain forest subject to intense logging within the Imataca Forest Preserve (Figures 2&3), east of El Palmar at the border between Bolivar state and Delta Amacuro territory, Venezuela. Field observations consisted of mapping foraging activity, recording prey, baiting the ants with prey and sugar water, monitoring workers' attempts to carry food in groups, and completely dissecting the nest. A portion of the colony was taken alive for laboratory bioassays.[19]

While compiling data on the occurrence of group transport among ants, I found information in the literature to be fragmentary and furthermore confused by the frequent usage of "group retrieval" for group transport (the former term is often used simply to indicate that multiple food items are

Figure 1.
Cross section of tree with Daceton armigerum *colony, revealing a segment of the nest.*
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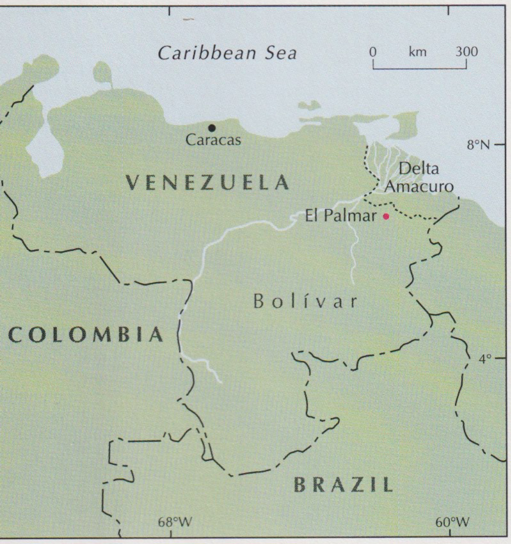

Figure 2 (above).
The study area was east of El Palmar at the border between Bolivar state and Delta Amacuro territory, Venezuela.

Figure 3 (opposite page).
Site of Daceton armigerum *colony near a logging road in Venezuela. The nest was in the tree at right. The trunk trail extended through the fallen vegetation at left.*

retrieved along a common route). Therefore the presence of group transport in each genus was confirmed through correspondence with 43 experts.

Results

The ants nested 6.5 m aboveground within the trunk of a healthy 10-m-tall tree. The trunk was 10 cm in diameter at breast height and 7 cm in diameter near the nest. The hollow core was hard and dry, forming a single smooth-walled chamber 120 cm long and ≤ 5 cm wide, packed with ants, reproductive (male and queen) brood, and worker brood (Figure 1). Nooks and crannies in the wood at either end of the main chamber were also occupied by ants and brood. The colony contained one dealate (wingless) queen, 2342 adult workers, and 18 alate (virgin) queens.

Most foragers in the Venezuelan colony were faithful to a 22-m-long trail, which was apparently unbranched except for a 1-m-long side route. (However, other foraging could have occurred out of view in the canopy above the nest entrance.) The route descended the nest tree, then meandered across a series of felled trees. This main route (or "trunk trail" *sensu* Hölldobler[12]) was stable during the two observation days, with most ants crossing within a centimeter of felt-tip pen marks made at three widely separated points along the route. Foragers were sparse: Typically one to six ants passed by per minute at the nest-tree base. Trail usage decreased with distance from the nest as ants gradually dispersed into the surrounding vegetation to forage.

Although the trunk route extended along fallen branches at ground level, workers seemed to shy away from soil. The longest journey onto the ground that I noted lasted just a few seconds—and the ant went only 2 cm before scurrying back to its branch. This confirms E. O. Wilson's view that *Daceton* is strictly arboreal.

Many workers gathered at sugar-water bait placed near the trunk route. Accumulation of these workers was slow because of the sparsity of ants available on the route. Ants eventually used a common path between trunk route and bait, indicating that a chemical recruitment trail had been deposited.

During the two field days, I recorded ants carrying 11 caterpillars, one adult fly (probably a tachinid), and a microlepidopteran moth. Ants on the trail snapped up pierid butterflies (Figure 4) and a beetle larva presented to them alive with forceps.

All prey but the microlepidopteran were carried by groups of workers, ranging from two to six ants (Figure 5). Usually these groups were exceedingly poorly coordinated. Two of the caterpillars were carried for at least two hours of my observations, and every one had been battered as if it had been pulled in conflicting directions over long periods. Indeed, often little progress was made until workers settled into a walking pattern that allowed forward motion at a pace of ~2 cm/s. However, transport frequently halted again whenever another ant attempted to join in, disrupting the pattern.

Workers carried brood during the nest dissection. Group transport of immatures sometimes occurred (Figure 6), particularly for the bulky reproductive immatures. This was more prompt and less fitful than food carriage, with workers seemingly having less difficulty coordinating their actions (but transport still seemed more antagonistic than is typical of, say, the army ants).

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Figure 4.
A Daceton armigerum *worker attacking a butterfly that had been placed before it by the author. The ant successfully killed the much larger butterfly and it was carried to the nest with the aid of three to five additional workers.*

Discussion

FORAGING PATTERN AND RECRUITMENT IN *DACETON* ANTS

My field observations largely confirm those made by E. O. Wilson[37] on *Daceton armigerum* in Surinam and Trinidad. Yet Wilson found no sign of foraging trails in his two colonies. The trail of the Venezuelan colony was stable for the two days of observations, suggesting that *Daceton* develop long-term trails ("trunk" trails) like those of certain *Pogonomyrmex*[12] or *Pheidole militicida.*[18] As in these examples, the *Daceton* trail appeared to be maintained largely in response to patches of highly dispersed food. The trail led into an area of felled trees; a rich supply of insect prey presumably lived scattered in the smashed foliage. Foragers spread out from the trails to search individually for food.

It remains to be seen whether *Daceton* also normally uses its trail system to exploit conjunct food patches (those within which little or no search time is necessary to find the individual food items[29]). Canopy homopteran colonies may represent such a source of food; W. Bodkin (in W. C. Crawley[5]) recorded *Daceton* tending coccids. Workers in our

Figure 5.
Group transport of a caterpillar by four Daceton armigerum *workers under undistubed field conditions.*

colony responded strongly to sugar water, evidently laying down trails to each sugar bait.

B. Hölldobler, J. Palmer, and M. W. Moffett[19] found a diversity of pheromonal sources in laboratory studies of the same colony as that in this paper. Trails made from poison-gland contents (associated with the sting) last at least a week under laboratory conditions and are presumably therefore a major contributor to the stable trail documented in the field. The contents of another gland for ants—the sternal gland—also produce trails, although transient ones (effective for minutes). These authors recorded recruitment to termite prey in the laboratory. They also demonstrated that the mandibular glands have an alarm function, while the pygidial gland contents elicit attraction.

Recruitment in the tribe Dacetini was previously known only for *Orectognathus* (the sister genus to *Daceton*), in which trails are laid from the contents of worker pygidial glands.[14] The workers use trails during nest emigrations but apparently never in harvesting food, which depends solely on individual initiative. *Orectognathus* is also the only other dacetine taxon with appreciable worker size variation, showing a less extreme version of the polymorphism seen in *Daceton*.[2]

Table 1. **Ant Genera that Exhibit Group Transport**

FAMILY GENUS	ITEMS BORNE BY GROUPS	EFFICIENCY	SELECTED REFERENCES
PONERINAE			
Leptogenys	food	good	D. J. C. Fletcher,[7] U. Maschwitz & M. Mühlenberg[23]
Mesoponera	food	good	C. Agbogda[1]
Onychomyrmex	food	good	correspondence with B. Hölldobler & R. Taylor, 1991
Paltothyreus	food	poor	B. Hölldobler[17]
Plectroctena	food	good	D. J. C. Fletcher[7]
Rhytidoponera	food	good	correspondence with R. H. Crozier & P. J. M. Greenslade, 1991
LEPTANILLINAE			
Leptanilla	food	poor	correspondence with K. Masuko, 1991
DORYLINAE			
Aenictus	food	good	J. W. Chapman[3]
Dorylus	food	good	W. H. Gotwald[9]
ECITONINAE			
Eciton	food, brood	good	N. R. Franks[8]
Labidus	food	good	C. Rettenmeyer[32]
Neivamyrmex	food, brood	good	correspondence with C. Rettenmeyer, 1991
Nomamyrmex	food	good	correspondence with C. Rettenmeyer, 1991
MYRMICINAE			
*Aphaenogaster**	food	good	B. Hölldobler[13]
Daceton	food, brood	poor	M. W. Moffett,[27] E. O. Wilson[37]
Leptothorax	food	poor	conversation with S. Cover, 1991
Lophomyrmex	brood	poor	M. W. Moffett[26]
Myrmica	food	good	J. H. Sudd[34]
Novomessor	food	good	B. Hölldobler et al.[20]
Oligomyrmex	food	poor	M. W. Moffett[24]
Pheidole	food	good	J. H. Sudd[33]
Pheidologeton	food, brood, adult workers, enemies, refuse, building material	good	M. W. Moffet[24,29]
Proatta	food	poor	M. W. Moffett[25]
Solenopsis (subgenus *Solenopsis*)	food	poor?	W. S. Creighton[6]
Tetramorium	food	good	correspondence with J. Traniello, 1991
Trigonogaster	brood	good	personal observation
Wasmannia	food	poor	D. B. Clarke et al.[4]
PSEUDOMYRMECINAE			
Pseudomyrmex	enemies, adult workers	poor	correspondence with D. H. Janzen, 1991
DOLICHODERINAE			
Azteca	food	good	correspondence with C. Rettenmeyer, 1991
Conomyrma	food	poor	personal observation
ANEURETINAE			
Aneuretus	food	good	J. F. A. Traniello & A. K. Jayasuriya[36]
FORMICINAE			
Anoplolepis	food	good	personal observation
Camponotus	food	good	conversation with B. Hölldobler, 1991
Formica	food	good	J. H. Sudd[34]
Lasius	food	good	J. F. A. Traniello[35]
Myrmecocystus	food, slaves	good	B. Hölldobler[15]
Oecophylla	food	good	B. Hölldobler[16]
Paratrechina	food	poor	personal observation
Prenolepis	food	good	conversation with B. Hölldobler, 1991

*Including *Novomessor* (conversation with B. Hölldobler, 1991)

DISTRIBUTION OF GROUP TRANSPORT OF FOOD AMONG ANTS

Group transport is known in 39 genera (of ~300[21]) in nine of the 11 extant subfamilies of the Formicidae (Table 1). The list is certainly incomplete because most authors have shown little concern with recording this behavior. Still, at least with regard to carrying food, those ant species capable of group transport are unquestionably in the minority. Most ants appear totally unable to do it, as may be the case, for the large pantropical tribe dacetini with the single exception of *Daceton*.

There is variation even within many genera. In three ecologically dominant taxa (the two largest ant genera, *Pheidole* and *Camponotus*, and Asian *Leptogenys*) my own field tests indicate a wide variation in skill, from a total lack of the activity to consistently high efficiency. Even army ants, generally among the premiere group transporters, have exceptions: Some African *Aenictus* species carry burdens no larger than single ants[10,11] and thus are unlikely to retrieve food in groups.

Without doubt the group transport of food has arisen independently in numerous phylogenetic lines. It tends to be associated with large colonies (populations at least in the thousands), elaborate recruitment systems, and the dietary importance of prey—characteristics prominent in taxa where group transport is most pronounced, such as weaver ants (*Oecophylla*, Figure 8), marauder ants (*Pheidologeton*), and army ants (Dorylinae and Ecitoninae).

One species generally treated as primitive (*Aneuretus simoni*) has small colonies but shows group transport,[22] while many species in the phylogenetically advanced genera *Monomorium* and most *Solenopsis* (fire ants) live in big colonies but do not. Yet, as might be expected, ants lacking mass recruitment (rapid deployment of numerous workers, often by means of pheromonal trails) consistently lack group transport of food, among them species restricted to recruitment by adult transport or tandem running.[13]

Group transport is the conveyance of a burden by two or more individuals. 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, many recent reviews of ant foraging strategies ignore group transport.[29:386]

GROUP TRANSPORT WORKS BEST WITH CERTAIN TYPES OF FOOD

Why do so few ants show group transport? Perhaps because some foods are better subjects for this behavior than others.

Items handled by groups usually come in discrete packages within a size range that groups can handle (Figure 7); examples are brood (during emigrations) and food such as small seeds or invertebrate prey (the latter in *Daceton*). Such items can be transported as they are. Items that are too large, or are exceptionally moist or crumbly (like rotting carcasses or fruit) tend to be eaten on the spot or gnawed into fragments taken singly. It may be easier for ants to dissect unwieldy food into fragments than to carve out big chunks of a size transportable by groups; consider the simple way in which fungus-growing ants (*Atta*) slice consistently-sized pieces from leaves to carry solitarily.[21]

Absence of group transport can often be explained by diet. Many fire ants scavenge for decayed foods that can be apportioned quickly in situ. *Lophomyrmex* ants look like ideal candidates for group transport, having large colonies, efficient mass recruitment, and the ability to gang-kill big prey; but their finely serrate mandibles permit them to chop prey up so swiftly that group carriage is never used with food.[26]

There are no records of group transport in the subfamilies Nothomyrmeciinae and Myrmeciinae and the tribes Amblyoponini and Cerapachyini,

Figure 6 (upper left).
Group transport of a worker larva by Daceton armigerum *workers during nest disturbances by the author.*

Figure 7 (left).
Anoplolepis longipes *ants, like most ant species that exhibit group transport, carry moderately sized objects, up to about the size of this roach in Sri Lanka.*

With respect to burden size and the numbers of ants that can join forces, group transport is best developed in Pheidologeton *and* Oecophylla, *perhaps followed most closely by certain army ants.*[29:386]

Figure 8.
Weaver ants (Oecophylla smaragdina) *can carry huge objects, such as this dead, weirdly-flanged walking stick in Australia (the prey's head is at left).*

Figure 9.
Minor and major workers of Pheidologeton pygmaeus *readily group transport colony brood during a nest emigration.*

but these ants specialize in killing prey small enough to be handled by single workers. Most dacetines, solitary foragers, similarly rely on individual stealth and strength to capture and transport small prey, rather than on group action.[21] Evolution of group transport in other predators—like army ants (Dorylinae and Ecitoninae), many ponerines, *Pheidologeton*,[29] and *Daceton* in the Dacetini—is correlated with elaboration of recruitment behavior and dietary expansion into larger prey.

GROUP TRANSPORT OF IMMATURES IN ANTS

Although seldom recorded, group transport of brood is probably widespread. Reproductive immatures are usually larger than workers; moving them during nest floods or other emergencies may require gang retrieval. When reproductives are similar in size to workers (as in *Myrmecia*), group transport is probably absent.

In *Daceton*, group transport of larvae and pupae is accomplished more skillfully than that of food. In *Pheidologeton pygmaeus* the difference is even more extreme:[28] Minors jointly carry major and alate brood with ease (Figure 9) while completely failing at group transport of food. Large hunks of food tend to be pulled in conflicting directions in groups until fragmented or eaten on the spot.[29] This should not be surprising. There is no alternative to group transport in moving a bulky immature, but cooperation in carrying food is never necessary. Food can be torn asunder either before or after retrieval, the best method varying with the type of food, the worker force needed, and defense costs.[29]

Evolution of group food-retrieval entails changes in worker responses to food, including the postponement of dissection behavior, which some ants may have achieved poorly (as in *Daceton*) if at all (as in *Pheidologeton pygamaeus*). The transport of pupae and larvae does not entail such impediments. Group transport of immatures is likely the ancestral condition for most ants, with group food-transport derived from it whenever diet and mass recruitment behavior make it an effective strategy.

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