COLONY SIZE, COMMUNICATION AND ANT FORAGING STRATEGY*

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Introduction

Some 12,000 ant species are known by now, with colony sizes ranging from a few individuals to 20,000,000 individuals. What constraints does this vast range of colony sizes place on the systems of organisation that they use? Alternatively, how does this range of colony sizes reflect the different systems of organisation used? We shall examine these questions in relation to ant foraging strategy, which as well as being the most visible aspect of their activity illustrates most clearly the roles and limits of communication in their collective behavior.

This paper aims to verify a prediction of the following hypothesis (Pasteels et al. 1985; Deneubourg et al. 1986). In theory, the organization of a small insect society can rely on most individuals at any moment "knowing", principally by learning, what it must do, where it must go, etc., and the workers' behavior has a strong determinist component. In a large insect society organization by individual learning is harder to achieve (Deneubourg et al. 1987). The workers' behavior is necessarily more random and their coordination becomes a major problem. To cope with this, a completely different organisational system is added to that already in place. This supplementary system is based on the complex collective structures, patterns and decisions that spontaneously emerge from simple autocatalytic interactions between numerous individuals and with the environment, mediated by essentially chemical communication (see, e.g., Pasteels et al. 1987; Goss and Deneubourg 1989; Beckers et al. in press; Deneubourg et al, 1989, in press; Goss et al. 1990).

The prediction that follows from this hypothesis is that the larger the colony size, the less foraging is individually based and the more

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the individual foragers are coordinated by mass chemical communication.

We shall use the following categories of foraging strategy that, as shall be discussed below, represent a crescendo of the integration of the individual forager into a network of communication: individual, recruitment, trunk trail and group hunting, their definitions being inspired by the work of different authors (e.g. Rosengren 1971; Wilson 1971; Leuthod 1975; Maschwitz 1975; Oster & Wilson 1978; Moffet 1988; Traniello 1989).

By individual foraging we mean foraging without systematic cooperation or communication in the discovery, capture or transport of prey items. Each forager leaves the nest, searches for food and transports it individually (e.g. *Cataglyphis bicolor, Pachycondyla apicalis*).

By foraging with recruitment, we mean that a scout having discovered a food item returns to the nest and transmits the information concerning its location to inactive foragers waiting in the nest. These recruits can become recruiters in their turn. It should be noted that recruiting species rely to a large extent on individual foraging for the discovery and exploitation of small sources.

Roughly speaking, three recruitment types can be distinguished. With tandem recruitment, the scout guides one recruit to the food item, with or without trail laying (e.g. *Leptothorax* sp.). With mass recruitment, a trail laid by the recruiter while returning to the nest guides recruits to the food (e.g. *Solenopsis invicta, Monomorium pharaonis*). Invitation by the recruiter in the nest is often active. With group recruitment, the scout guides a group of nestmates, in some cases (if not all) laying a pheromone trail to the nest (e.g. *Tetramorium caespitum, Camponotus socius*). However, as every species that we know uses group recruitment also uses a more or less efficient mass recruitment, we shall refer to group/mass recruitment. Note that some authors distinguish a fourth recruitment system, group raiding (type IV—Oster and Wilson 1978), which is characterised by a very strong invitation and recruitment trail that results in a large group of recruits leaving the nest together in a rush. We have included this system in group/mass recruitment.

With trunk trails, semi-permanent trails guide foragers to long-lasting food sources (e.g. many *Formica* sp.), and also serve as starting-off points for individual foragers, which may also recruit to the trunk-trails. Finally, group hunting foragers (sensu Moffet 1988, including army ants) leave the nest and forage collectively in a swarm along a well-defined trail system that is constructed as the swarm progresses (e.g. *Dorylinae* sp.).

These descriptions are by no means meant to be definitive, and there are of course species whose foraging does not fall neatly into one or indeed any of these categories. Nevertheless, as shall be discussed below, they represent a crescendo of the integration of the individual forager into a network of communication. Other recruitment systems are known to exist (such as short-distance recruitment or non-directional recruitment), but for lack of data have been omitted. Similarly, the colony sizes given are average figures, obtained by different techniques, and generally with rather small sample sizes. Polycalic societies pose a special problem. For these reasons, the values quoted must be considered only as first-order approximations.

Results and Discussion

Table 1 presents the colony size and foraging system of 98 different species. Fig. 1 presents the foraging system as a function of the colony size. Although that data base is small compared to the number of known ant species, a distinct trend is clear (note the logarithmic scale). The smaller societies rely on individual foragers that do not transmit their discoveries. The largest societies rely on permanent chemical communication between the individuals. Between these two limits, one finds the different types of recruitment. Again, the smaller recruiting societies rely on a slow, individual recruitment, where a recruiter interacts directly with one or a few individuals. The larger recruiting societies rely on the faster mass recruitment, where one recruiter can interact via a chemical trail with a large number of potential recruits. The trail transmits both the position of the source and that of the nest to the recruits. Note that we have listed the species in Table 1 by alphabetical order for facility, and that the same tendency appears in each sub-family.

Taking these results into consideration we propose two extreme blueprints for the way in which ants organise their foraging.

The first blueprint consists of small societies which rely on the capacity for learning of its members to exploit the foraging area efficiently. Individual foragers, for example, develop fidelity to parts of their foraging area and can orient themselves over large distances (Wehner et al. 1983; Fresneau 1985). They do not interact directly with each other, nor do they communicate their food discoveries, yet they are capable of dividing the foraging area amongst themselves (Deneubourg et al. 1987). The society may be considered to have placed its complexity at the level of the individual.

The second blueprint consists of large societies whose individual behavior may be considered as simple. They rely on a highly developed network of chemical communication based on permanent trail-laying behavior to coordinate the foragers' activity and to aid their orientation. Their capacity for individual orientation is limited not only because it is not so needed as the trails are there, but also because too much individuality could prevent collective foraging from functioning efficiently. It is surely no coincidence that the largest and most chemically integrated societies, i.e. the different army ants and termites, are practically blind. The colony size is large, not simply to ensure that their "inefficient" workers manage to perform the necessary tasks by sheer weight of numbers (Oster and Wilson 1978; Herbers 1981), but because they need a large reserve of individuals for the amplifying mechanisms (e.g. recruitment) by which they structure their foraging to work (e.g. Pasteels et al. 1987). The society may be said to have placed its complexity more at the level of the interactions between individuals.

Between these two extremes, we find intermediate sized societies which rely on individual scouts to forage small food items and on recruitment to amplify the information relating to important food sources. The sequence tandem/group-mass/mass is characterised by an increasing number of individuals that react to the recruiters' signals, and is associated with an increasing colony size. In mass recruiting species there is a tendency in the largest societies to lay trail pheromone not only when returning with food but also when leaving the nest and more or less continually in the foraging area (e.g. *Pheidole militicida* - Hölldobler and Möglich 1980; *Iridomyrmex humilis* - Van Vorhis Key and Baker 1986; Aron et al. 1989).

There is of course a large degree of overlapping between the different categories in fig. 1. This is to be expected whenever one tries to categorize nature, but is also the result of imprecision in our knowledge of colony size, which is anyway highly variable for a

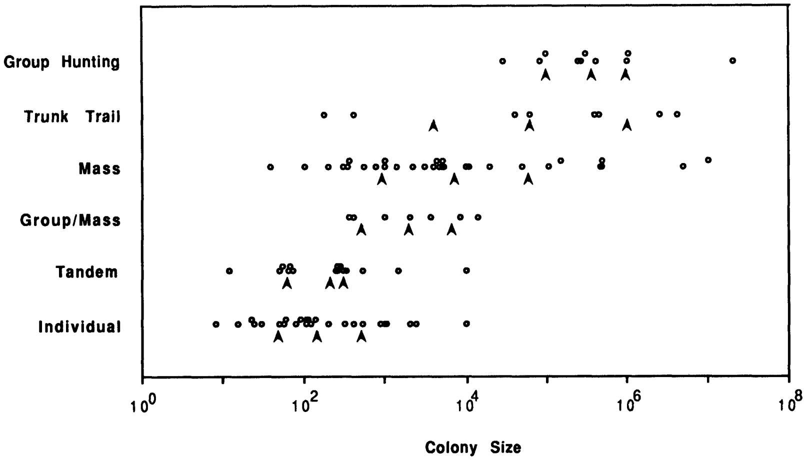

Fig. 1. Foraging strategy as a function of colony size for 98 ant species (see Table 1). The arrows mark the 25, 50 (median) and 75 percentiles.

given species. Furthermore, others factors such as the size, distribution and type of food exploited intervene, and ant foraging strategy and food type are obviously connected (e.g. Carrol and Janzen 1973; Traniello 1989).

Other less precise data confirm the tendency seen in fig. 1. For example we know that *Crematogaster ashmeadi* colonies are very large and that they use mass recruitment (Leuthold 1968a, b), whereas *Bothroponera tesserinoda* colonies are small and use tandem recruitment foraging.

The same overall tendency as shown here for ant species, also noted by Buschinger (1980) for dulotic ants, is well known in the Apidae. Species with small colonies, such as bumblebees, use an individual foraging strategy. Those with large colonies, such as honeybees, melipones and trigones, use recruitment (Lindauer and Kerr 1958; Seeley 1985). The tendency is also observed in terns (Erwin 1978).

We would like to end this paper with an appeal to readers to help us increase the size of our data base. We would welcome any information about colony size and foraging system, whether for species already in Table 1 or for any other ant species.

Table 1. Average colony size and foraging strategy of 98 ant species. The subfamilies (in brackets) are: 1 = Aneuretinae, 2 = Cerapachyinae, 3 = Dolichoderinae, 4 = Dorylinae, 5 = Formicinae, 6 = Leptanillinae, 7 = Myrmeciinae, 8 = Myrmicinae, 9 = Ponerinae, 10 = Pseudomyrmecinae. The foraging types are: I = Individual, TR = Tandem recruitment, GM = Group/Mass recruitment, MR = Mass recruitment, TT = Trunk trail, GH = Group hunting.

Species (subfamily)	Nest Size	Frg. Type	References
Acromyrmex landolti (8)	1,000	MR	Jaffe pers. comm.
octospinosus	50,000	MR	Blum et al. 1964; Jaffe pers. comm.
Aenictus laeviceps (4)	85,000	GH	Schneirla 1965
Amblyopone pallipes (9)	15	I	Traniello 1978; Lachaud pers. comm.
Aneuretis simoni (1)	40	MR	Traniello and Jayasuriya 1981; Jayasuria and Traniello 1985
Anomma nigricans (4)	1,036,800	GH	Vosseler 1905
wilverthi	20,000,000	GH	Raignier and van Boven 1955
Atta cephalotes (8)	500,000	MR	Jaffe and Howse 1979; Jaffe pers. comm.
sexdens	5,000,000	MR	Riley et al. 1974; Jaffe pers. comm.
texana	10,000,000	MR	Moser and Blum 1963; Riley et al. 1974; Jaffe pers. comm.
Azteca foreli (3)	50,000	MR	Jaffe pers. comm.;
Camponotus aethiops (5)	2,500	I	Suzzoni pers. comm.
pennsylvanicus	2,200	MR	Pricer 1908; Traniello 1977
sericeus	250	TR	Hölldobler et al. 1974
truncatus	50	I	Suzzoni pers. comm.
Cataglyphis bicolor (9)	2,000	I	Wehner et al. 1983
cursor	1,000	I	Cagniant 1983; Lenoir pers. comm.
Conomyrma bicornis (3)	5,000	MR	Jaffe pers. comm.
Crematogaster sumicrasti (8)	1,000	MR	Jaffe pers. comm.
Cyphomyrmex rimosus (8)	100	I	Blum et al. 1964; Jaffe pers. comm.
Daceton armigerum (8)	10,000	I	Blum and Portocarrero 1965; Jaffe pers. comm.
Diacamma rugosum (9)	100	I	Fukumoto and Abe 1983
Dinoponera australis (9)	30	I	Fowler 1985
quadriceps	60	I	Dantas de Araujo pers. comm.
Eciton burchelli (4)	425,000	GH	Schneirla 1957
hamatum	300,000	GH	Schneirla 1957; Rettenmeyer 1963
rapax	275,000	GH	Sudd and Franks 1987
Ectatomma ruidum (9)	125	I	Lachaud et al. 1984
Erebomyrma nevermanni (8)	180	TT	Wilson 1986

Table 1. Continued

Species (subfamily)	Nest Size	Frg. Type	References
Formica aquilonia (5)	400,000	TT	Zakharov 1978
bruni	1,400	MR	Cherix and Maddalena-Feller 1987
cunicularia	1,100	I	Deffernez pers. comm.
fusca	500	MR	Wallis 1964; Möglich and Hölldobler 1975
lugubris	40,000	TT	Rosengren 1971; Breen 1979
polyctena	450,000	TT	Rosengren 1971; Kruk-de-Bruin et al. 1977; Horstmann 1982
pratensis	60,000	TT	Rosengren 1971; Jensen 1977
rufa	4,000,000	TT	Gösswald 1951; Rosengren 1971
yessensis	51,000	TT	Ito 1973; Cherix 1987
Iridomyrmex humilis (3)	150,000	MR	Keller pers. comm.
Labidus praedator (4)	1,000,000	GH	Rettenmeyer 1963
Lasius fuliginosus (5)	2,500,000	TT	Hainaut-Riche et al. 1980; Quinet et Pasteels 1987.
niger	5,500	MR	Stradling 1970; Brian 1977
Leptogenys chinensis (9)	367	GM	Maschwitz and Schönegge 1983
ocellifera	50,000	MR	Maschwitz and Mühlenberg 1975
Leptothorax acervorum (8)	250	TR	Dobrzanski 1966; Büschinger 1971; Möglich et al. 1974; Möglich 1979
ambiguus	50	TR	Talbot 1965; Möglich 1979
curvispinosus	50	TR	Headley 1943; Talbot 1965; Möglich 1979
duloticus	12	TR	Talbot 1957; Alloway 1979; Möglich 1979
longispinosus	65	TR	Headley 1943
muscorum	300	TR	Büschinger 1966; Möglich et al. 1974
nylanderi	280	TR	Plateau pers. comm.
unifasciatus	325	TR	Lane 1977; Plateau pers. comm.
Messor barbara (8)	8,000	GM	Delye pers. comm.
sancta	3,500	GM	Delye pers. comm.; Suzzoni pers. comm.
Monomorium pharaonis	800	MR	Peacock et al. 1955; Sudd 1960
Myrmecia gulosa (7)	900	I	Haskins and Haskins 1950; Robertson 1971
Myrmica rubra (8)	1,000	GM	Stradling 1970; Petal 1972; Cammaerts and Cammaerts 1980
ruginodis	2,000	GM	Stradling 1970, Brian 1972; Cammaerts and Cammaerts 1980
sabuleti	3,000	MR	Brian 1972; Cammaerts and Cammaerts 1980

Table 1. Continued

Species (subfamily)	Nest Size	Frg. Type	References
Myrmicaria eumenoides (8)	20,000	MR	Levieux 1983
Myrmoteras barbouri (5)	8	I	Moffet 1986a
toro	22	I	Moffet 1986a
Neivamyrex nigrescens (4)	30,000	GH	Topoff et al. 1980
Novomessor cockerelli (8)	350	MR	Hölldobler et al. 1978.
albicetosus	350	MR	Hölldobler et al. 1978.
Ocymyrmex barbiger (8)	200	MR	Marsh 1985
Odontomachus bauri (9)	300	I	Jaffe and Marcuse 1983
haematoda	500	TR	Hölldobler and Engel 1978; Jaffe pers. comm.
troglodytes	240	TR	Dejean 1982; Dejean and Bashingwa 1985
Oecophylla longinoda (5)	480,000	MR	Way 1954; Hölldobler and Wilson 1978
Ophthalmopone berthoudi (9)	400	I	Peeters and Crewe 1987
Ologomyrmex overbecki (8)	400	TT	Moffet 1986b
Pachycondyla apicalis (9)	90	I	Lachaud et al. 1984; Fresneau 1985
caffraria	70	TR	Lévieux 1967; Agbogba 1981
commutata	400	GM	Mill 1982, 1984
obscuricornis	100	I	Traniello and Hölldobler 1984; Fresneau 1984
villosa	500	I	Lachaud et al. 1984; Lachaud pers. comm.
Pheidole embolopyx (8)	300	MR	Wilson and Hölldobler 1985
fallax	10,000	MR	Law et al. 1965; Jaffe pers. comm.
pallidula	5,000	MR	Detrain pers. comm.
Pheidologeton diversus (8)	250,000	GH	Moffet 1988
silenus	100,000	GH	Moffet 1988
Pogonomyrmex badius (8)	4,300	MR	Brian et al. 1967; Hölldobler and Wilson 1970
californicus	4,500	MR	Hölldobler and Wilson 1970; Erickson 1972
occidentalis	3,880	MR	Lavigne 1969; Hölldobler and Wilson 1970
Ponera eduardi (9)	1,500	TR	Le Masne 1952; Bernard 1968
Proatta butteli (8)	10,000	MR	Moffet 1986c
Pseudomyrmex termitarius (10)	75	TR	Jaffe pers. comm.
triplarinus	10,000	TR	Jaffe pers. comm.
Serrastruma lujae (8)	57	I	Dejean 1982
serrula	78	I	Dejean 1982

Table 1. Continued

Species (subfamily)	Nest Size	Frg. Type	References
Smithistruma emarginata (8)	199	I	Dejean 1982
truncatidens	133	I	Dejean 1982
Solenopsis invicta (8)	100,000	MR	Wilson 1962; Tschinkel 1987
Tapinoma erraticum (3)	1,000	MR	Meudec 1979; Verhaeghe et al. 1980
Tetramorium caespitum (8)	14,000	GM	Brian et al. 1967; Pasteels et al. 1987
Trachymyrmex urichi (8)	100	MR	Jaffe and Villegas 1985; Jaffe pers. comm.
Zacryptocerus varians (8)	1,000	MR	Wilson 1976; Jaffe pers. comm.

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Summary

The foraging strategy of 98 ant species is examined in relation to their colony size. Six foraging strategies are distinguished, namely indivdual, tandem, group/mass and mass recruitment, trunk trail, and army ant type, and are seen to be associated with increasing colony size. This supports the hypothesis that the larger the colony, the more the individual worker is integrated into a network of chemical communication. Two extreme organisational blueprints are proposed. The first consists of small societies which rely on the capacity for learning of its members to exploit the foraging area efficiently. The second relies on the complex collective patterns that spontaneously emerge from chemically mediated recruitment processes interacting with the environment.

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