Size and behavior in ants: Constraints on complexity

(behavioral repertoire/brain volume/insects/allometry/social behavior)

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ABSTRACT   In this paper I investigate the behavioral complexity of ants in relation to brain size. The volume of the corpora pedunculata, involved in the selection of motor programs, and the antennal lobes, involved in processing olfactory information, are directly related to the volume of the brain of an ant. The volume of the optic lobe, involved in visual processing, is not related to total brain volume. Brain volume is allometrically related to head width in ants. Behavioral complexity, as assayed by the size of the behavioral repertoire within the nest, is directly related to the cube of head width. Behavioral complexity is thus related to the 3/2 power of brain volume. The size of the behavioral repertoire does not appear to correlate with any ecological characteristics of the species but may be a passive consequence of body size. Determination of body size by numerous ecological factors may place constraints on the complexity of behavior that an ant can achieve.

Size has profound implications for most aspects of the biology of organisms, including mechanical design, shape of the organism, generation time, longevity, and fecundity (1). The size of the brain, as well as of other organs, varies with body size in animals. There have been attempts to document a relationship between behavioral complexity and relative brain size in a variety of organisms, including primates (2), bats (3), and other mammals (2, 4). However, these studies have been limited by the lack of an objective criterion by which to measure behavioral complexity.

In this paper, I shall first review current information on brain size in ants and the relationship to body size. I shall then describe a method by which behavioral complexity can be objectively measured in ants and show that behavioral complexity is directly related to the size of the ant.

Brain Size in Ants

Pandazis (5) measured the brain volumes of 39 species of ants and the volumes of several distinct brain regions: the optic lobes, the antennal lobes, and the corpora pedunculata. The corpora pedunculata in an insect brain appear to function in the selection of motor programs and the formation of behavior sequences (6, 7) such as learning (8). The relationship between the volume of the corpora pedunculata and the volume of the brain is apparently linear (Fig. 1). Fitting the data to a power function does not produce a better fit ($r^2 = 0.91$ for myrmicines and 0.96 for formicines).

The antennal lobes of the ant brain are involved mainly in processing olfactory information (7). The relation between antennal lobe volume and total brain volume is given in Fig. 2. In this case the myrmicines and formicines show the same relationship. Again a power-function regression provides only a marginal increase in the amount of variance explained ($r^2 = 0.98$).

The most deviant point in Fig. 2 (arrow) is for data from *Formica sanguinea*, a facultative slave-making species (9). Workers of this species are able to carry out all normal colony functions in the absence of slaves. They do not show the degeneracy of behavior of the obligate slave-making species of *Polyergus*. However, they have an unusual type of olfactory communication system involving the production of "propaganda substances" (10), which produce alarm disorientation in the species they enslave. It is not known whether there is a direct connection between these observations.

The optic lobe in ants is involved in processing visual information. As seen in Fig. 3, there is no apparent relation between the size of the optic lobe and the size of the brain. This is in accord with Pandazis' (5) conclusion that there was no relationship between the size of the corpora pedunculata and the size of the optic lobe. Olfactory cues are vastly more important to ant behavior than visual cues (9, 11), and this seems to be reflected in brain structure.

Pandazis did not measure the head sizes of the ants whose brain volume he measured. I measured the head width across the eyes for 15 of Pandazis' species that are represented in collections in the Museum of Comparative Zoology (Harvard University). For each species that had a simple caste system (so that brain size could be associated to caste) 10 specimens were measured. The relation between head width (HW) and brain volume (BV) is shown in Fig. 4 and is well described by the allometric relation BV = 0.016 (HW)$^{1.96}$ ($r^2 = 0.89$, $P < 0.001$).

Measurement of Behavioral Complexity

The behavioral complexity of the ants used in this analysis is the size of the behavioral repertoire as estimated by the Fagen–Goldman method (12, 13). The Fagen–Goldman method relies on fitting the observed frequency distribution of behavioral acts in behavioral categories to a lognormal distribution.

That the frequency distribution of categories of behavior is described by a lognormal distribution is not unexpected (14, 15) and appears to be true in a diversity of situations for human children, rhesus monkeys, and ants (12, 13). For ants it is practical to obtain behavioral catalogues for a number of species. In 10–50 hr one can observe 2000–4000 behavioral acts and obtain an estimated sample coverage of 0.9995 or better. A sample coverage of this value implies that observation of 10,000 more behavioral acts will produce five acts that do not fit into categories of behavior already seen. When one obtains this level of sample coverage, it is usually possible to estimate accurately the total size of the behavioral repertoire. This procedure is equivalent to integrating the lognormal distribution that provides the best fit to the data on behavioral frequency.

This study is limited to species in which workers show little size variation. Not included are species in which the workers exhibit some sort of continuous size polymorphism [*Formica perpilosa* (16), *Atta sexdens* (17), *Orectognathus versicolor* (18), and *Cephalotes atratus* (19)]. Two species, *Leptothorax*
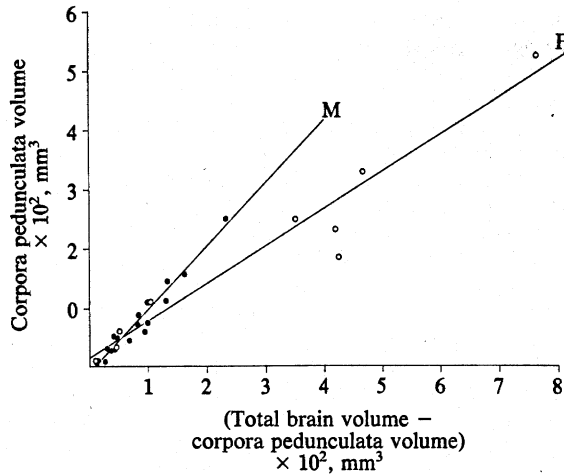
FIG. 1.   Relation between the volume of the corpora pedunculata (CP) and the volume of the brain (BV) for 9 species of Formicinae (F) and 17 species of Myrmicinae (M) (from data in ref. 5). Lines obtained by least-squares analyses of the data are described by the equations CP = 1.07(BV − CP) − 0.001 (r^2 = 0.96) for M and CP = 0.64(BV − CP) − 0.0009 (r^2 = 0.93) for F.

longispinosus (20) and *L. ambiguus* (21) were excluded for several important reasons. These data (20, 21) were collected in a manner that is not comparable to any other data set. A number of "activities" such as "rest," "movement," and "antennate with worker" were catalogued that have not been catalogued by anyone else, to my knowledge. When such activities, together with behavior occurring outside the nest, are excluded in order to make the data sets comparable, there are too few remaining behavioral acts to allow one to draw any conclusions. There were nine species available for analysis. Five species had a strictly monomorphic caste system, *Solenopsis molesta* (D. Allen, personal communication), *Xenomyrmex floridanus* (22), *Leptothorax curvispinosus* (12), *Crematogaster ashmeadi* (22), and *Amblyopone pallipes* (23). Four species had a completely dimorphic caste system with a generalized minor worker caste and a specialized major worker caste. The repertoire of the minor worker caste was used in *Aneuretus simoni* (24), *Pheidole dentata* (25), *Camponotus* (*Colobopsis*) sp. (22, 26), and *Zacryptocerus varians* (22, 26, 27).

For the above nine species, the size of the behavioral repertoire was recalculated for that subset of the behavior
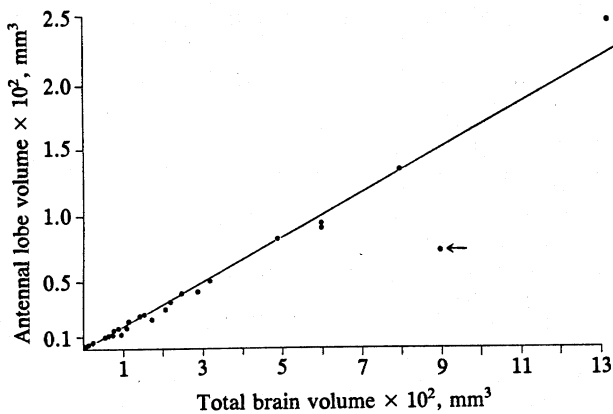

FIG. 2.   Relation between antennal lobe volume (AL) and total brain volume (BV) in Formicinae and Myrmicinae (from data in ref. 5). The deviant point (arrow) is due to data for *Formica sanguinea*, a facultative slave-making species. Line is described by AL = 0.18(BV) − 0.0004 (r^2 = 0.96).
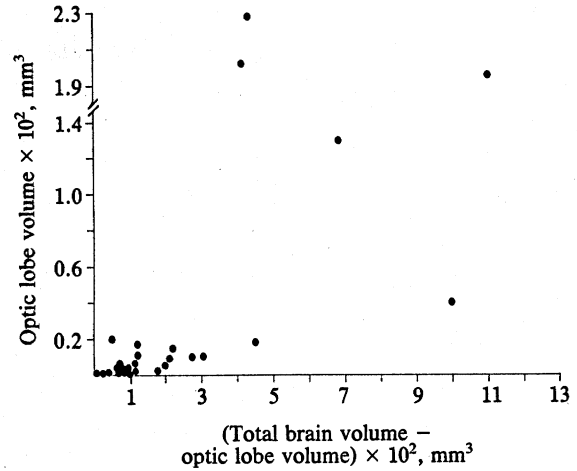

FIG. 3.   Optic lobe volume vs. the volume of the remainder of the brain for myrmicine and formicine ants (from data in ref. 5).

which occurred within the nest. Head width across the eyes was measured for 10 workers of each species.

The estimated behavioral repertoire sizes range from 25.0 (*A. simoni*) to 41.8 categories of behavior (*Z. varians*). Although it is possible to fit a significant linear regression to the data set, there is clearly some sort of curvilinear relation between head width and behavioral repertoire size. In Fig. 5, behavioral repertoire size (BR) is shown as a function of the cube of head width (HW). The least-squares regression is BR = 12.3(HW)^3 + 24.4 (r^2 = 0.92, P < 0.001).

Discussion

There are at least three possible explanations for the positive relationship between head size and behavioral complexity in ants. The first is that the phenomenon is an artifact of observation. It may be easier to discriminate more different kinds of behavior in large species than in small ones. This explanation is highly unlikely because all observations were made under dissecting microscopes, in which the relative visual size of the ant is held nearly constant.

The second explanation is an essentially ecological one. Large species may need to perform a wider variety of tasks in order to survive than small species. This explanation seems unlikely for this data set because behavioral observations were limited to behavior taking place solely within the nest. Since the individuals with whom the ants were interacting were of the same species (other worker ants, eggs,
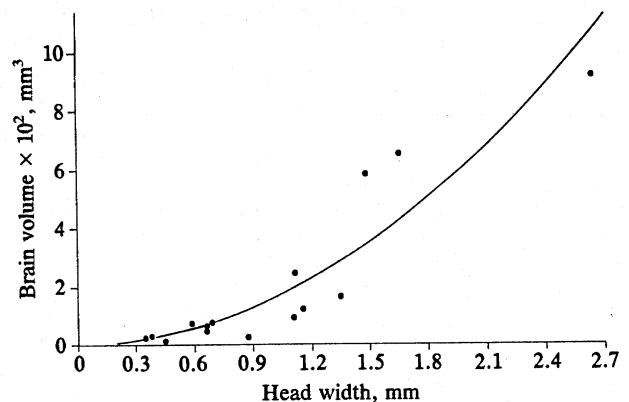

FIG. 4.   Allometric relation between head width (HW) and brain volume (BV) for 15 species of ants. Curve is described by the function BV = 0.016(HW)$^{1.964}$ (r^2 = 0.89).
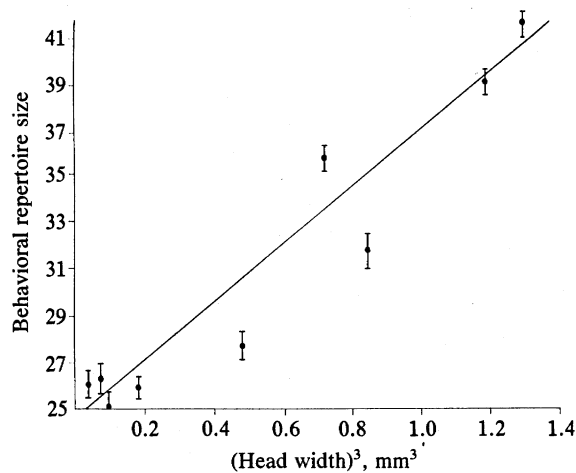
FIG. 5. The estimated size of the behavioral repertoire (BR) (and 95% confidence limits) as a function of the cube of the head width (HW). BR = 12.3(HW)^3 + 24.4 (r^2 = 0.92).

larvae, and pupae), one would not expect an increase in size to increase behavioral options toward those individuals.

The categories of behavior that are added to the repertoire do not seem to require increased body size. All ants share certain categories of behavior. Indeed, it is difficult to imagine how an ant could be an ant without certain categories of behavior. First, there are the categories involving the care of the brood: carrying and licking eggs, larvae, and pupae; feeding the larvae; and assisting larval ecdysis, adult eclosion, and meconium removal. Second are the grooming categories: self-grooming and allogrooming workers and the queen. Third are various feeding categories: oral trophallaxis, feeding on insect remains, and eating other types of solid material within the nest. Here there is some variability (e.g., *Amblyopone* does not engage in oral trophallaxis; *Zacryptocerus* does not bring insect remains into the nest), but all ants seem to have some behavior in this group.

For larger species there are novel categories of behavior. In two species (*Camponotus* sp. and *Zacryptocerus*) there is a traffic in infrabuccal pellets (26) involving feeding on them, sharing them with other workers, and feeding them to larvae. In *Zacryptocerus* there are several categories involving abdominal trophallaxis (22, 25). In *Amblyopone* there are several categories of behavior involving different types of brood care. These novel categories of behavior do not seem to be a function of body size, nor do they seem to be inherently more complicated. There are simply more of them.

The ants for which data are available form a diverse group. There do not seem to be consistent ecological correlates with increased size (Table 1). There are both large and small terrestrial species, species that live in preformed plant cavities on the ground, and arboreal species. There are both small and large species with dimorphic caste systems and small and large species with monomorphic caste systems. The repertoire size of the most conspicuous predator, *A. pallipes*, is very similar to the least predatory ant, *Z. varians* (39.0 and 41.8 categories of behavior, respectively).

A third possible explanation is that behavioral complexity is restricted by the size of the ant brain. Small species do not perform as many categories of behavior as large ants. That larger species perform more categories of behavior may be simply a result of more neurons. There is suggestive evidence for this hypothesis. Larger brains do, in fact, mean more neurons. Calyx cells have been shown to vary in size between insect orders (29) but to be fairly consistent within narrower taxonomic groups. Larger ants have larger brains (Fig. 4). Brain volume is roughly proportional to the square of head width, whereas repertoire size is proportional to the cube of head width. Thus (brain volume)$^{3/2}$ is approximately proportional to repertoire size. Over the range of repertoire sizes of 25–40 categories, this relation is virtually indistinguishable from a straight line.

Howse (6) suggested that the size of the corpora pedunculata varied with head width but not with apparent behavioral complexity. However, there could be no quantitative assessment of the complexity of behavior in a single context, and the work was based on qualitative comparisons between insects of many orders. Corpora pedunculata volume in ants is proportional to brain volume (Fig. 1) and is thus related to repertoire size in the same manner as is brain volume. Because the corpora pedunculata have been implicated in the coordination and control of complex motor patterns, they seem likely candidates to account for differences in the size of the behavioral repertoire.

The volume of the antennal lobe is also highly correlated with brain volume (Fig. 2). It seems unlikely that increased antennal lobe size, perhaps correlating with increased ability to process olfactory information, can directly account for differences in behavioral complexity, though it is a possibility. Optic lobe volume, however, does not correlate with total brain volume.

The causal determinants of the relationship between body size and brain size are unknown. The size of an organism is the complex result of many, perhaps conflicting, selective pressures. Size may have phylogenetic constraints and may be affected by nest site, potential predators or competitors, the type of food eaten, or the size of the colony, to name but

Table 1. Species whose behavioral repertoires were included in this study

Species	Scavenger or predator	Method of recruitment to food sources	Nest site	Activity	Reference
Monomorphic worker caste					
Solenopsis molesta	Both	Trails	Soil	Diurnal	D. Allen*
Xenomyrmex floridanus	Both	Trails	Trees	Diurnal	22
Leptothorax curvispinosus	Both	Tandem running/trails	Preformed plant cavities on ground	Diurnal	12
Crematogaster ashmeadi	Both	Trails	Trees	Diurnal	22
Amblyopone pallipes	Predator	Solitary	Soil	Diurnal	23
Dimorphic worker caste					
Aneuretes simoni	Both	Unknown	Preformed plant cavities on ground	Diurnal and nocturnal	24
Pheidole dentata	Both	Trails	Soil	Diurnal	25
Camponotus (Colobopsis) sp.	Both	Trails	Trees	Diurnal	22, 26
Zacrypocerus varians	Both	Solitary + trails	Trees	Nocturnal	22, 26, 27

*Personal communication.

several. Whatever the selective pressures involved, once body size is determined, brain size is constrained. Once brain size is determined, the size of the behavioral repertoire also may be constrained. Thus the 1.7-fold difference between the number of categories of behavior of the largest repertoire and the smallest repertoire may be a passive consequence of larger size.

Ecology, caste, and communication surely have an effect on the size of the behavioral repertoire of ants. However, in this study there is no clear-cut correlate of large behavioral repertoire other than large size. Detailed studies of similarly sized ant species may reveal more about other correlates of repertoire size. Such studies would be similar to previous analyses of residuals (2). Wilson (28) presents data on the behavioral repertoire of 10 species of *Pheidole*. Although the data are not completely comparable to those used in this study, there is no size-related behavioral-complexity increase. It is possible that the range of head size (about 0.4 mm) is not enough to produce a size relationship but does show variability as a function of ecology, caste, and communication system.

It is conceivable that one of the selective pressures to increase body size may be to increase the number of categories of behavior of which an ant is capable. However, change in body size will alter relationships to predators, prey, competitors, nest sites, colony-founding mode, and life-history patterns. Here it is well to be reminded that brain size (or perhaps corpora pedunculata size) could increase under selection without head- and body-size increase. Increased behavioral complexity can only be one of a large number of selective pressures on body size. It is likely that greater changes in behavioral complexity will be produced by changing body size for other, ecological reasons than would be produced by selection on behavioral complexity itself.

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