



Evolution of brain size in class-based societies of fungus-growing ants (Attini)

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A social lifestyle is often assumed to be more complex than a solitary one, due to social demands that may require increased cognitive capabilities. These nested assumptions underlie hypotheses to explain a correlation between brain size and group size in social vertebrates, using group size and accumulation of social traits, as alternative proxies for social complexity. Eusocial insects challenge the generality of the hypothesis that social complexity relies on increased cognitive capabilities of individuals. We used data from previously published studies to test for an association between sociality and brain size across 18 species (nine genera) of fungus-growing ants (Attini), which range from basal taxa with fewer than 100 monomorphic individuals, to derived colonies containing several million polymorphic, highly specialized individuals. Among monomorphic species, increased colony size was associated with decreased relative brain size and increased olfactory lobe size, although the latter result was sensitive to both the exclusion of potential outliers and whether phylogenetically independent contrasts were used. Within leafcutters (*Atta*), the relative size of the antennal lobes was also associated with group size, but may also reflect ecological foraging specialization, which may be a confounding variable. Comparisons between class- and individual-based societies highlight the general problem of increasing social structure in proportion to group size and show that there are alternative solutions to this problem: one alternative involves increasing behavioural specialization of individuals and evolved rules; the other involves increased diversification of individual behaviour, social norms and ultimately institutions.

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Behavioural interactions are central to group living (Konner 2010), and thus, sociality is often thought to require an increase in cognitive capabilities to successfully navigate these interactions (e.g. Humphrey 1976; Dunbar 2003; Byrne & Corp 2004; Dunbar & Shultz 2007; for an invertebrate example see: Smith et al. 2010; for critiques see: Holekamp 2006; Barret et al. 2007; Farris & Schulmeister 2011). Such reasoning has been used to help explain the disproportionately large brain size of social vertebrates, especially primates and humans ('social brain hypothesis') (dolphins: Marino 1996; bats: Barton & Dunbar 1997; primates: Dunbar 2003; birds: Beauchamp & Fernández-Juricic 2004; hyaenas: Holekamp 2006; ungulates: Shultz & Dunbar 2006; for a general review, see de Waal & Tyack 2003).

The social brain hypothesis assumes that (1) individuals closely track the myriad social relationships of individuals within their group, including social rank (Bergman et al. 2003), and (2) a more complex social environment requires an increased neural investment to track social relations (see discussion in Konner 2010). Thus,

'all socially living species should show enlarged brain sizes relative to more solitary congeners' (Barret et al. 2007, page 561). The generality of these hypotheses is open to question because studies are overwhelmingly biased towards vertebrates that live in social groups in which individuals are treated as individuals (i.e. in individualized societies).

Social invertebrates provide exceptional opportunities to understand possible links between sociality and brain evolution. In many cases, invertebrate sociality rivals that of vertebrates in organizational structure (Wilson 1975), yet there is significant variation in recognition mechanisms that facilitate social organization (Fletcher & Michener 1987). In a social sweat bee (*Lasiosglossum*, Halictidae), for example, mechanisms of kin recognition and discrimination use individual-level signals, as do most vertebrate kin recognition systems, while those of honeybees (*Apis*, Apidae) or many ants (Formicidae) use colony-level signals (see e.g. Fletcher & Michener 1987; Tang-Martinez 2001). In other words, individuals are treated as individuals in individualized societies, and as members of a group in class-based (nonindividualized) societies. In the latter, there frequently is further specialization beyond that between reproductive and nonreproductive tasks, such that workers are further specialized to perform only a subset of the worker tasks (Anderson & McShea 2001; Hölldobler &

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Wilson 2009). An increase in task specialization with increasing group size is a recurrent pattern in many social insects, as it is in human societies (Naroll 1956; Bonner 1993; Gell-Mann 2011). In general, the relationship between relative brain (or brain region) size and sociality is largely an open question for insects (Gronenberg & Riveros 2009). Most research has focused on one clade within the insect order Hymenoptera (Aculeata: bees, wasps and ants), within which sociality has evolved repeatedly (Wilson 1971). Earlier studies suggested that the corpora pedunculata (mushroom bodies), which is the brain region associated with multisensory integration and learning (Heisenberg 1998), was especially enlarged in social species (Dujardin 1850; Howse & Williams 1969; Howse 1975; see Gronenberg & Riveros 2009). A recent, comprehensive study of hymenopteran mushroom bodies included both aculeate and nonaculeate taxa, and showed that relative enlargement of the mushroom bodies significantly predated cladogenesis leading to the Aculeata (Farris & Schulmeister 2011). Thus, enlarged mushroom bodies were part of the aculeate ground plan, which subsequently gave rise to social forms. With respect to the social brain hypothesis, the new findings by Farris & Schulmeister (2011) demonstrated that the baselines for mushroom body size and complexity have shifted upward within Hymenoptera. Consequently, any size increases putatively associated with sociality must exceed those that already evolved in parasitic Hymenoptera (Euhymenoptera), presumably associated with learning of host location and identity. These important new findings, however, do not negate the potential applicability of the social brain hypothesis, because they do not preclude size increases above the shifted baseline in social forms (e.g. comparing social and solitary females within a single facultatively social species; Smith et al. 2010). Furthermore, it is important to recognize that the social brain hypothesis, as currently construed, has been developed for species exhibiting individualized societies; hence a direct test in class-based (nonindividualized) societies is complicated by other factors (below).

In contrast to individualized societies, in class-based societies, such as those found in many insects, relative brain size has been hypothesized to increase in simple societies in which workers are generalists (Gronenberg & Riveros 2009). As the degree of social organization increases, and as workers are increasingly specialized, relative brain size is expected to decrease (Gronenberg & Riveros 2009). A corollary of the latter hypothesis is that the degree to which workers specialize on particular behaviours should be positively associated with a differential size increase of those particular brain areas that are functionally linked with the specialized behaviour.

To test the social brain hypothesis, social organization has been measured indirectly, often using group size, based on the rationale that the number of individual behavioural interactions increases exponentially with group size (Dunbar 1992, 1998, 2003). There is, however, no unanimity as to whether group size is a reliable or comparable descriptor of social organization across diverse taxa (e.g. Byrne & Bates 2007). Larger group size is also associated with changes in qualitative social organization in humans (Carneiro 1967, 2000). For instance, larger human societies have greater task specialization, as demonstrated by number of occupations in different-sized settlements (Naroll 1956; Bonner 1993). In class-based societies, such as those of many insects, colony size has been strongly linked to organizational complexity, including more pronounced behavioural specialization of workers, which sometimes evolved into morphological specialization (Hölldobler & Wilson 1990; Anderson & McShea 2001). Under the assumptions of the social brain hypothesis as presented for vertebrates (Table 1), group size should not necessarily correlate with relative brain size in class-based societies. In such societies, individuals face fewer cognitive challenges vis-à-vis sociality, because recognition is based on group identity, not individual identity (see Fletcher & Michener 1987). Furthermore, in class-based groups social competition occurs at group levels (e.g. members of different patrines compete to rear reproductives from their own line; Makert et al. 2006).

Fungus-growing ants (*Attini*) live in class-based agricultural societies in which group size spans more than four orders of magnitude, from fewer than 100 monomorphic workers per colony to several million polymorphic workers (see Supplementary Material for a précis of their natural history). Social structure also varies among taxa and includes traits such as worker–queen dimorphism, monogyny (a single queen), nestmate recognition, behavioural specialization, and in the derived leaf-cutting genera, *Atta* and *Acromyrmex*, strong polymorphism within the worker caste (Hölldobler & Wilson 1990, 2009). This variation allows us to analyse the relationships between relative brain size, size of the antennal lobes (primary olfactory centres in the insect brain) and colony size for class-based insect societies (see Table 1 for predicted patterns according to different hypotheses).

We tested the hypothesis that, in fully eusocial species, relative brain size decreases as colony size increases, due to the positive association between colony size and degree of behavioural specialization among workers (see Gronenberg & Riveros 2009). We used data on the relative size of the antennal lobe to test the idea that a specific brain region will increase in size if individuals are highly specialized on tasks that require information processed by that brain region. Thus, we predicted two opposite patterns:

Table 1
Summary of hypothesized and observed results based on the vertebrate-derived social brain hypothesis (SBH) and as hypothesized for social insects by Gronenberg & Riveros (2009)

Measure of brain	Effect of colony size		Index based on a scalogram	
	Hypothesized	Observed	Hypothesized	Observed
Relative brain mass	None according to assumptions of the vertebrate SBH Significant negative association based on Gronenberg & Riveros (2009)	Significant quadratic association including all species Significant negative linear association excluding <i>Atta</i> and <i>Acromyrmex</i>	Significant	Significant linear association including all species
Antennal lobe volume	None according to assumptions of the vertebrate SBH Significant positive association based on Gronenberg & Riveros (2009)	Significant negative linear association including all species Significant quadratic association excluding <i>Apterostigma</i> Significant negative within <i>Atta</i> genus	Significant	Not tested
Number of glomeruli	None according to assumptions of the vertebrate SBH Significant positive association based on Gronenberg & Riveros (2009)	Nonsignificant including all species Significant quadratic association before but not after phylogenetic control and excluding <i>Apterostigma</i>	Significant	Not tested

a decrease in relative brain size as colony size increases, but an increase in relative size of the antennal lobes in larger colonies with more specialized workers.

Acknowledging that variation in social organization involves many more traits than colony size, we assessed whether an alternative quantification of social organization would yield results similar to those observed when relying on colony size alone. Previously, scalograms have been used in cultural anthropology as a measure of social complexity (e.g. Carneiro 1962; Carneiro & Tobias 1963), but they can also be used to detect regularities in human social organization (Gell-Mann 2011). We scored our taxa for the occurrence of socially relevant qualitative traits and constructed a scalogram (Guttman 1944), which ranks different societies by the relative frequency of occurrence of preselected traits, enabling comparisons of the relative number of components that characterize social organizations.

METHODS

Data Sources and Study Taxa

We obtained data on relative brain mass for 18 species across nine genera in the ant tribe Attini from Seid et al. (2011). The glomeruli of the antennal lobes are the brain regions primarily responsible for processing olfactory inputs. We obtained the relative sizes of the antennal lobes (antennal lobe/optic lobe) and number of glomeruli for 25 species in nine attine genera from Kelber et al. (2009). Since each glomerulus receives projections from neurons expressing a single receptor gene (Galizia & Menzel 2001), the number of glomeruli might be associated with diversity of chemical information processed, whereas the ratio of the size of antennal lobe to the size of the optic lobe provides a measure of the relative investment made for processing olfactory input. Data on colony sizes were taken from the literature, or obtained from specialists (Supplementary Table S1). When information on colony size for a species was not found (or taxonomic identification was limited), we used the average colony size calculated from other species within the genus.

Scalogram Construction

We used a method from cultural anthropology (Carneiro 1962; Carneiro & Tobias 1963) to derive a measure of social complexity based on the construction of a scalogram (Guttman's scale; Guttman 1944), which uses the relative frequency of occurrence of preselected social traits to characterize social complexity. We selected information about traits to be included from a list of 57 social traits compiled from a review of specialized journals over a 5-year block, and from consultation with specialists (see Supplementary Material for details). From this list we removed traits that were clearly irrelevant to attine societies; some of the traits were modified to the form 'presence-absence' and others were categorized using a specified number of bins. Thus, we included group size, worker-queen dimorphism, haplometrosis (solitary colony foundation), monogyny (a single queen), age polyethism, recruitment, nestmate recognition, mass communication, territoriality, group foraging, worker polymorphism and multiple mating.

Data Analyses

We log transformed all data. We then performed ordinary least squares correlations between colony size and three brain-related variables: (1) total brain mass, (2) relative size of antennal lobe (= antennal lobe/optic lobe) and (3) number of glomeruli. Similarly, we correlated the accumulated number of social traits from

the scalogram analyses with these three brain-related variables. Following visual inspection of the plots, we analysed data with and without potential outliers (also indicated in figures). All analyses were performed using the statistical software JMP 8.0.2 (SAS Institute Inc., Cary, NC, U.S.A.). We also used phylogenetic independent contrast (PIC) analyses to take into account the effect of nonindependence due to phylogenetic relationships across species. PIC analyses were performed using the log-transformed data analysed with the PDAP module in MESQUITE v. 2.72 (Maddison & Maddison 2007) and used the phylogeny of the tribe Attini reconstructed by Schultz & Brady (2008). Species-level analyses of *Atta* are based on the phylogeny hypothesized by Bacci et al. (2009). All statistical results reported include output with and without PIC analysis. Figures are based on observed traits values, not values from phylogenetic contrasts (for merits of the two contrasts, see Ricklefs & Starck 1996).

RESULTS AND DISCUSSION

Among attine species there was a significant quadratic association between relative brain size and colony size ($R^2 = 0.56$, $N = 18$, $P = 0.005$; after PIC: $R^2 = 0.52$, $P = 0.006$; Fig. 1a, Table 1), which

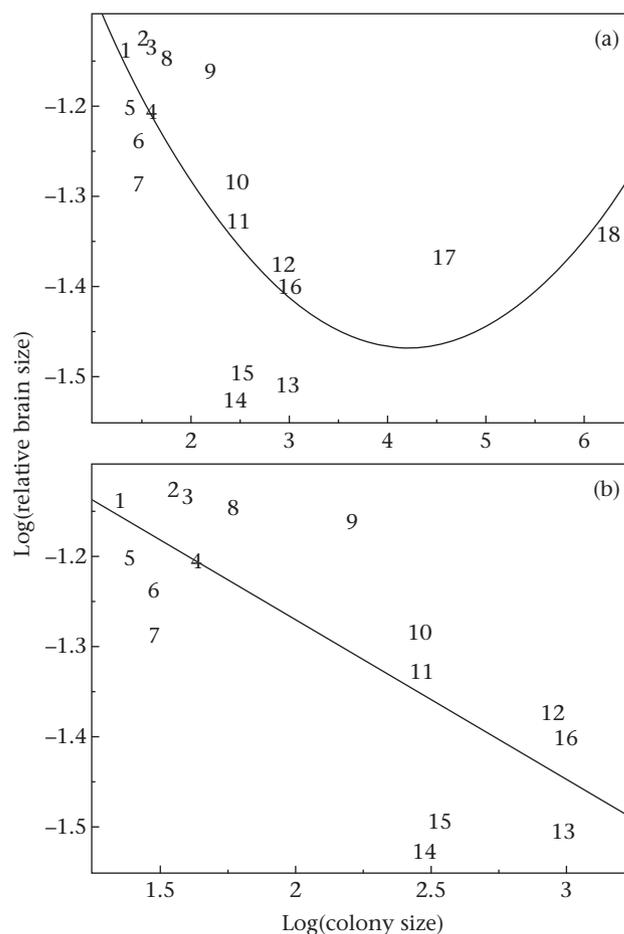


Figure 1. Correlation between colony size and relative brain size in fungus-growing ants (Attini). (a) Includes all species examined. (b) Excludes *Atta colombica* and *Acromyrmex echinator*. 1: *Cyphomyrmex longiscapus*; 2: *Cyphomyrmex* sp. 1; 3: *Cyphomyrmex costatus*; 4: *Cyphomyrmex muelleri*; 5: *Apterostigma* sp. 2; 6: *Apterostigma* sp. 1; 7: *Apterostigma* sp. 3; 8: *Myrmicocrypta* cf. *ednaella*; 9: *Mycocarpus smithii*; 10: *Trachymyrmex cornetzi* sp. 1; 11: *Trachymyrmex cornetzi* sp. 2; 12: *Trachymyrmex* BH; 13: *Trachymyrmex* sp. 10; 14: *Trachymyrmex zeteki*; 15: *Mycetophylax* sp.; 16: *Sericomyrmex* sp.; 17: *Acromyrmex echinator*; 18: *Atta colombica*. See text for sources of data.

provided a better fit than a linear equation ($R^2 = 0.24$, $N = 18$, $P = 0.039$), but was marginally nonsignificant after PIC correction ($R^2 = 0.19$, $P = 0.07$). This association was strongly affected by two species, *Acromyrmex echinator* and *Atta colombica*, which are leafcutter species with huge colonies that are commonly described as ‘superorganisms’ (Hölldobler & Wilson 2010). Average relative brain sizes of these two species are similar to that of *Trachymyrmex* BH, whose colony sizes are several orders of magnitude smaller. For extremely polymorphic species, however, the biological validity of an ‘average’ trait is dubious (below). Indeed, whereas absolute brain size varies by more than one order of magnitude among the 18 species studied, the entire range is found in *Acromyrmex echinator* (0.006–0.255 mg; Seid et al. 2011) and the full range of relative brain size (brain mass/body mass) occurs within *Atta colombica* (0.0048–0.0952 mg of brain/mg of body mass; Seid et al. 2011). When *Atta* and *Acromyrmex* species were excluded from analyses, there was a significant negative association between brain and colony size across the monomorphic species ($R^2 = 0.60$, $N = 16$, $P < 0.001$; after PIC: $R^2 = 0.55$, $P = 0.001$; Fig. 1b).

As for primates (see Introduction), fungus-growing ants also showed an association between group size and brain size, yet it followed a quadratic function in ants, suggesting the existence of a switch point where the trend was reversed, such that quantitative changes lead to qualitative changes in social evolution (Carneiro 2000; Read 2002). Below the switch point, relative brain size decreased with increasing colony size. This observation is consistent with the hypothesis that relative brain size should decrease with increasing social organization in class-based societies (Gronenberg & Riveros 2009), in which workers specialize on a subset of behavioural tasks, so that a relatively small brain presumably could sustain the performance of fewer behaviours (Oster & Wilson 1978; Bourke 1999; Anderson & McShea 2001).

A corollary of this hypothesis (Gronenberg & Riveros 2009; Table 1) is that different degrees of behavioural specialization should be associated with differential development of those brain areas that are involved in generating those specialized behaviours (for a general discussion of this expected association, see Eberhard & Wcislo 2011). Consistent with this hypothesis, the specialized foragers of leafcutter ants (*Atta*) that follow chemical trails to and from their nests differed from other workers in attributes of the antennal lobe glomeruli, suggesting that there may be ‘neuroanatomical subcastes’ (Kleineidam et al. 2005, 2007; Kuebler et al. 2010).

Large class-based insect societies rely heavily on chemical communication (Wilson 1975; Hölldobler 1995), as do most of those species with individualized societies (Fletcher & Michener 1987). Larger societies, however, will have increased numbers of interactions with external environmental features (e.g. food resources or pathogens that are advertently or inadvertently brought to the nest), and so increases in colony size may lead to chemically more diverse nest environments, which in turn may require an increase in information-processing capacity, by analogy to arguments linking brain size to habitat complexity, or ecological foraging specializations (see below). For attines, the relative antennal lobe size was significantly linearly associated with group size ($R^2 = 0.39$, $N = 14$, $P = 0.016$; dashed line in Fig. 2a), although no such correlation was observed using PIC ($R^2 = 0.17$, $N = 14$, $P = 0.149$). Group size was not correlated with number of glomeruli ($R^2 = 0.02$, $N = 20$, $P = 0.52$; Fig. 2b). In both cases, *Apterostigma* deviated strongly from the general pattern. When we excluded *Apterostigma* as an outlier, the number of glomeruli ($R^2 = 0.47$, $N = 19$, $P = 0.007$) increased in small colonies but then decreased in large colonies, although no such result was observed using PIC ($R^2 = 0.15$, $N = 19$, $P = 0.24$). Excluding *Apterostigma*, relative antennal lobe size significantly increased in small colonies and then decreased in large colonies both without PIC ($R^2 = 0.76$, $N = 13$,

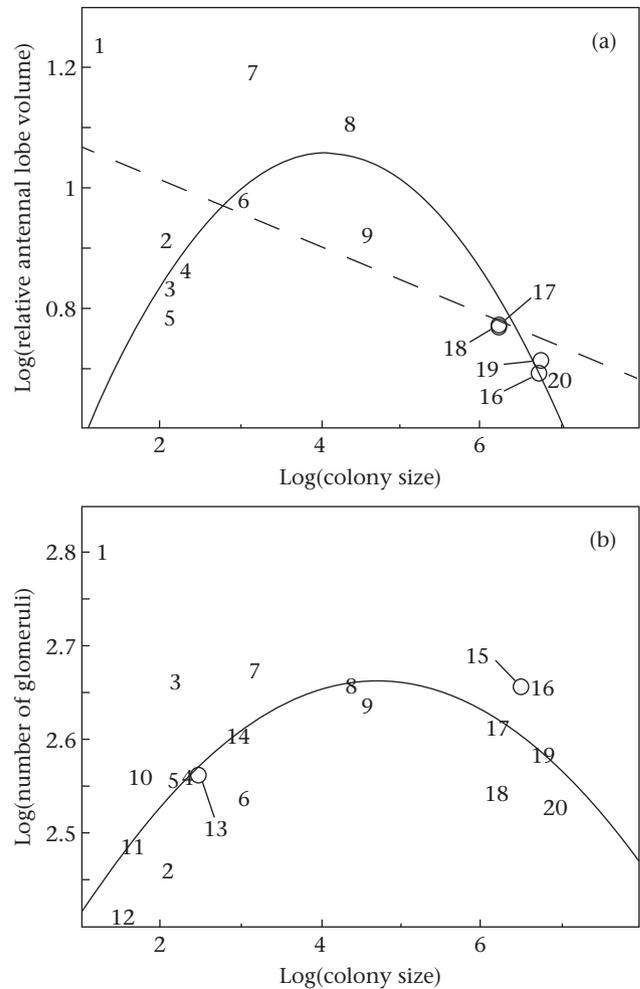


Figure 2. Correlation between colony size and (a) relative antennal lobe size and (b) number of glomeruli in fungus-growing ants (Attini). (a) Showing all species examined (dashed line) and excluding *Apterostigma mayri* (solid curve). Quadratic correlations in (a) and (b) exclude *A. mayri*. 1: *Apterostigma mayri*; 2: *Mycetophylax conformis*; 3: *Myocepurus smithii*; 4: *Trachymyrmex septentrionalis*; 5: *Myocepurus* sp.; 6: *Sericomyrmex amabilis*; 7: *Acromyrmex lundii*; 8: *Acromyrmex heyeri*; 9: *Acromyrmex octospinosus*; 10: *Cyphomyrmex minutus*; 11: *Mycetosoritis hartmanni*; 12: *Cyphomyrmex costatus*; 13: *Trachymyrmex cornetzi*; 14: *Acromyrmex balzani*; 15: *Atta laevigata*; 16: *Atta vollenweideri*; 17: *Atta colombica*; 18: *Atta cephalotes*; 19: *Atta sexdens*; 20: *Atta texana*. See text for sources of data.

$P = 0.001$) and with PIC ($R^2 = 0.50$, $N = 13$, $P = 0.021$). A biological justification for excluding *Apterostigma* as an outlier is tenuous, although some members in this genus (the *pilosum* group) differ from all other attine ants in that they cultivate a pterulaceous fungi, and a veil-like sheet surrounds the fungus garden (Villesen et al. 2004; Pitts-Singer & Espelie 2007). Although sample sizes were small enough to violate statistical assumptions, in the polymorphic leafcutter genus *Atta*, there was a significant association between log(relative antennal lobe size) and log(group size) ($R^2 = 0.95$, $N = 5$, $P < 0.0048$; Fig. 3), and a PIC analysis did not change the results ($R^2 = 0.96$, $N = 5$, $P = 0.0032$). In general, however, we lack the detailed quantitative and qualitative analyses of the information processed by ants of different sizes, which are needed to understand the relationship between task specialization and brain structure and function in polymorphic species.

Further study also is needed to relate information-processing needs to ecological specialization (Bernays & Wcislo 1994; Farris & Roberts 2005; Safi & Dechmann 2005; Shumway 2008; Farris & Schulmeister 2011). Variation in relative size of antennal lobes in

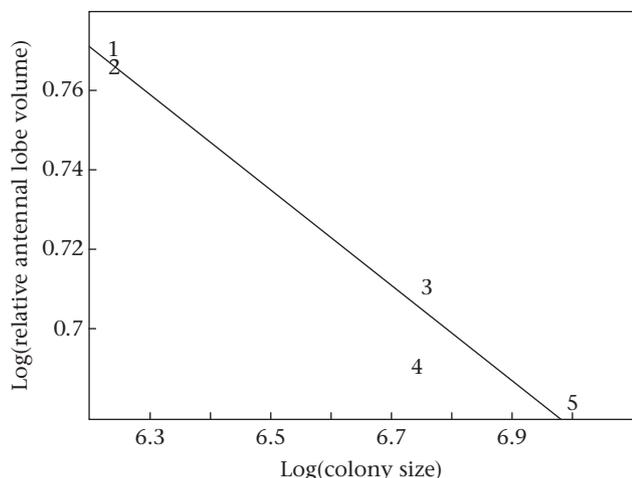


Figure 3. Correlation between colony size and relative antennal lobe size in fungus-growing ants in the genus *Atta*. 1: *A. colombica*; 2: *A. cephalotes*; 3: *A. sexdens*; 4: *A. vollenweideri*; 5: *A. texana*. See text for sources of data.

Atta may be associated with a more diverse plant odour environment, which arises from a more diverse leaf harvest. *Atta colombica* and *A. cephalotes* are sister species (Bacci et al. 2009) that occupy lowland Neotropical rainforests and harvest numerous species of plants (e.g. >140 species are harvested by *A. colombica* in a single locality: Shepherd 1985; see also Wirth et al. 2003), and both species have relatively large antennal lobes. In contrast, those species that have a low investment in antennal lobes tend to harvest and handle fewer plant species: *Atta vollenweideri* is a grass specialist (Röschard & Roces 2002) and *A. texana* occurs in more arid regions and extends into the southern U.S.A. (Weber 1972), where plant diversity is undoubtedly lower than in tropical regions. Finally, *A. sexdens*, although tropical, tends to favour drier habitats, and overall plant diversity is lower in tropical dry forests than in evergreen forests (Condit et al. 2010).

Group size is often used as a proxy for 'social complexity' because the number of social interactions is an exponential function of group size (Dunbar 1992, 1998, 2003), and pragmatically, such data are readily available. Recent findings, however, highlight the fact that group size is not a universal measure of social complexity (Byrne & Bates 2007). In fact 'social complexity' or 'behavioural complexity' is undefined or vaguely defined in many studies, and we lack biologically meaningful and universal operational definitions (see discussions in: Shumway 2010; Eberhard & Wcislo 2011), which has encouraged the exploration of additional descriptors of social organization for comparisons with brain size (Lehmann & Dunbar 2009; Lehmann & Ross 2011). In addition to variation in colony size, for example, attine ants also vary greatly in traits relating to social structure, including worker–queen dimorphism, monogyny, nest-mate recognition, behavioural specialization, and, in the derived genera *Atta* and *Acromyrmex* (leafcutter ants), strong polymorphism within the worker caste (Hölldobler & Wilson 1990, 2009).

The Attini scalogram reflects the existence of common social traits across the tribe, such as a lower limit to the size of mature colonies, and worker–queen dimorphism. The larger colony sizes are associated with additional social traits such as multiple mating, high degree of worker specialization and group foraging that appear to be restricted to one or two genera, *Atta* and *Acromyrmex* (e.g. Villesen et al. 2002). There is a general agreement with the overall ranking from the scalogram and phylogenetic patterns (cf. Schultz & Brady 2008; Mehdiabadi & Schultz 2010), even though the former is not intended to be informative about historical patterns or causality. The genus *Myrmicocrypta* deviates from

the observed pattern in that it has more traits than expected for its relative brain size (Fig. 4). Overall, we found a significant correlation between number of social traits and relative brain size across the 18 species (without PIC: $R^2 = 0.21$, $N = 18$, $P = 0.058$; with PIC: $R^2 = 0.30$, $N = 18$, $P = 0.018$); this correlation was much more evident when we treated *Mycetophylax* sp. as an outlier and removed it (Fig. 4; without PIC: $R^2 = 0.45$, $N = 17$, $P = 0.003$; with PIC: $R^2 = 0.51$, $N = 17$, $P = 0.001$).

Our survey makes a number of implicit assumptions that warrant further investigation. There are very few sociobiological studies for many species, and the behaviours of others are unknown, so in most cases little is known about intraspecific variation in behaviour, neuroanatomy, or basic demographic patterns. Most attines are monomorphic with relatively little variation in size among workers. In contrast, *Atta* and *Acromyrmex* are highly polymorphic (Hölldobler & Wilson 1990, 2009, 2010), so that the full range of body and brain size variation occurs within one taxon. Moreover, the smallest and largest ants are characterized by different allometries between body size and both head size (Wilson 1953) and brain mass (Seid et al. 2011), so measurements of 'average' sizes should be cautiously interpreted for these taxa. *Apterostigma mayri* also diverges strongly from the general pattern seen in other taxa, and it has the largest relative size of antennal lobes and the greatest number of antennal lobe glomeruli (Kelber et al. 2009). Whereas a large number of glomeruli hints at a capability to discriminate among a broad diversity of odours, there is little information on the chemical environment of *Apterostigma* (Singer & Espelie 1998; Pitts-Singer & Espelie 2007); as noted above, a subset of *Apterostigma* species cultivate a fungus in the Pterulaceae (Villesen et al. 2004), unlike other attines that cultivate a leucocoprineaceous fungus. Nevertheless, we found that generally the number of glomeruli does not correlate with colony size. Interpreting this lack of significance is complicated by the fact that recent studies show considerable variation within a single species, especially in those that are highly polymorphic (Kuebler et al. 2010), and we lack data that relate variation in glomeruli number to behavioural variation.

A consideration of social traits other than group size (Holekamp 2006; Shultz & Dunbar 2007) may be particularly important for social insects, because of the mix of class-based and individualized societies among taxa. Hence, group size as the sole metric potentially masks significant biological variation to a greater extent than in vertebrate societies. In sweat bees (Halictidae), for example, fully differentiated caste-based societies occur in groups having as few as two individuals (e.g. Wcislo et al. 2004), while other species have

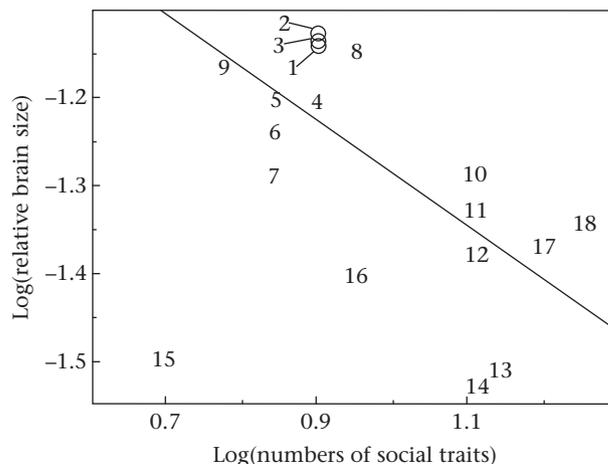


Figure 4. Correlation between relative brain size and number of social traits in fungus-growing ants (Attini). Species as in Fig. 1. See text for sources of data.

group sizes of more than 30 individuals yet there is no social differentiation at all (reviewed in: [Wcislo 1997](#); [Schwarz et al. 2007](#)). Unlike primates and other vertebrates, group size should be a weaker constraint in class-based insect species because cognitive load does not depend upon the number of individuals and interactions, but rather on the specific task(s) being performed. Therefore, our finding that colony size is associated with relative brain size suggests that the effect is due to other social traits that covary with colony size or are a consequence of colony size. Using a scalogram ([Carneiro 1962](#)), we found that the number of social traits was negatively correlated with relative brain size (see above), supporting the idea that behavioural specialization and relative brain size are more strongly correlated in more stratified societies. Scalograms enable one to partition social complexity into specific components, which allows a more detailed understanding of social organization ([Carneiro 1962, 1967, 1987](#); [Gell-Mann 2011](#)). Further research is needed to determine the amount and nature of information processed by an individual, and to what extent the addition of new social traits (e.g. new social roles, kin discrimination, nest architecture), relative to degree of task specialization, generates greater or lower cognitive loads.

Concluding Remarks

[Dunbar \(1992\)](#) noted that the link between brain size and behaviour can be construed as an information-processing problem, under the assumption that if there is more information to be processed and stored, then a larger neural substrate is required. If so, then an increase in colony size increases the cognitive load for each individual. This expectation is probably met for species characterized by individualized societies, but the pattern reverses in class-based societies for which behavioural specialization may be strong, because individual workers are more likely to be recognized as members of a group, not particular individuals within a group. The fact that colony size is negatively correlated with relative total brain size, and positively correlated with relative antennal lobe size, is consistent with this hypothesis. Cognitive demands associated with sociality raise problems that extend beyond group size, and a clearer understanding of the association between brain size and variation in social organization must incorporate additional factors ([Byrne & Corp 2004](#); [Shultz & Dunbar 2006](#); [Lehmann & Dunbar 2009](#)). A more complete framework to assess these factors might be provided by the use of scalograms, which help highlight social traits that are associated with brain development but make no assumptions about causality. Size matters ([Bonner 2006](#)), and, as pointed out by [Carneiro \(2000, page 12927\)](#), social evolution is the 'struggle to increase structure in proportion to size'. This general principle highlights both the commonalities of individualized and class-based societies and the divergence in their evolutionary trajectories to arrive at different solutions to the same problem. For individualized societies, such as primates, increasing social structure is associated with increasing behavioural capabilities of individuals, whereas in class-based societies such as ants, increasing social structure is associated with increased behavioural specialization, so any given worker performs fewer tasks overall. In both cases, relative brain size reflects adaptations to solve ecological problems that arise as a consequence of changing social organizations. Further comparisons of class-based and individualized societies promise to provide a more synthetic understanding of the interplay between the evolution of brain and society.

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Supplementary Material

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