

# Colony size, social complexity and reproductive conflict in social insects

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## Abstract

The broad limits of mature colony size in social insect species are likely to be set by ecological factors. However, any change in colony size has a number of important social consequences. The most fundamental is a change in the expected reproductive potential of workers. If colony size rises, workers experience a fall in their chances of becoming replacement reproductives and, it is shown, increasing selection for mutual inhibition of one another's reproduction (worker policing). As workers' reproductive potential falls, the degree of dimorphism between reproductive and worker castes (morphological skew) can rise. This helps explain why small societies have low morphological skew and tend to be simple in organization, whereas large societies have high morphological skew and tend to be complex. The social consequences of change in colony size may also alter colony size itself in a process of positive feedback. For these reasons, small societies should be characterized by intense, direct conflict over reproduction and caste determination. By contrast, conflict in large societies should predominantly be over brood composition, and members of these societies should be relatively compliant to manipulation of their caste. Colony size therefore deserves fuller recognition as a key determinant, along with kin structure, of social complexity, the reproductive potential of helpers, the degree of caste differentiation, and the nature of within-group conflict.

## Introduction

Research on social evolution in insects has concentrated on the origin of eusociality and on conflicts over reproduction and sex allocation within established societies (e.g. Bourke & Franks, 1995; Crozier & Pamilo, 1996; Choe & Crespi, 1997). A less well-explored theme is the transition from simple to complex sociality among social insects. By simple societies, I mean those with few or no morphological differences between reproductive individuals and workers, no physical caste polymorphism among the workers, and relatively simple nests and communication systems. By complex societies, I mean

those with wide morphological differences between reproductives and workers, worker polymorphism, and relatively complex nests and systems of communication. Previous authors have used similar terminology to classify the social organization of insects (e.g. Michener, 1974). The distinction between simple and complex societies corresponds to the traditional division of insect societies into 'primitive' and 'advanced' types (e.g. Wilson, 1971, p. 88), and to Kukuk's (1994) classification of them into 'behaviourally eusocial' and 'morphologically eusocial' forms. Complex societies almost certainly evolved from simple ones, since it is extremely unlikely that a complex society could evolve directly from a solitary ancestor. In fact, phylogenetic evidence suggests that the transition from simple to complex societies has occurred repeatedly within independent social insect lineages (e.g. termites: Noirot & Pasteels, 1988; ants: Hölldobler & Wilson, 1990, p. 26).

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In this paper, I explore the transition from simplicity to complexity in the social organization of insects and argue that a major determinant of social complexity is colony size. In particular, I develop the argument first made by Alexander *et al.* (1991) for a strong link between colony size, the reproductive potential of workers, the degree of caste differentiation and the nature of within-colony reproductive conflict. I present evidence that these traits covary in social insects, I suggest an additional reason (worker policing) why workers have reduced reproductive potential in large colonies and I describe causal feedback loops that reinforce the evolution of large colony size.

The transition from simple to complex insect societies is important because it is associated with the loss of 'totipotency', meaning the loss of the ability of individuals to adopt both reproductive and helper roles (Crespi & Yanega, 1995). Such a reproductive division of labour based on fixed morphological differences is the feature that sets apart the complex societies of insects. In the extreme case, the loss of totipotency results in an irreversibly sterile worker caste. The effect of colony size on insect social complexity is also an important theme because it helps explain the enormous social diversity among insects, and because of its relevance to more general ideas. These include the emergence of complexity in unitary, multicellular organisms (Bonner, 1988; McShea, 1996; Bell & Mooers, 1997), evolutionary transitions and the evolution of individuality at other scales of biological organization (Buss, 1987; Maynard Smith & Szathmáry, 1995; Michod, 1996, 1997), policing of selfish behaviour in social groups (Ratnieks, 1988; Frank, 1995; Reeve & Keller, 1997), and the occurrence of reproductive conflicts of interest within all types of society, including those of vertebrates (e.g. Alexander *et al.*, 1991; Ratnieks & Reeve, 1992; Keller & Reeve, 1994; Emlen, 1995).

### Ecological influences on colony size in social insects

The factors that determine mature colony size in social insects at the ultimate level, and those determining the spread of colony sizes across taxa and communities, have not been well studied. Several ecological advantages to large colony size have been proposed. These include increased defence, homeostasis and work ability (Wilson, 1971; Jeanne, 1991), greater ability to manipulate the surrounding environment (Wilson, 1990), more predictability in reproductive output (Wenzel & Pickering, 1991), higher sexual production and year-to-year survival (Schmid-Hempel *et al.*, 1993), better fighting ability (Franks & Partridge, 1993) and enhanced resistance to seasonal climates (Kaspari & Vargo, 1995). However, limits to colony size must also exist. For example, it may pay colonies to grow less in order to reproduce earlier, if this is beneficial in life-history terms (Oster & Wilson,

1978). Extra workers may produce no compensatory increase in per capita productivity beyond a certain colony size because of inefficiencies in task performance (Michener, 1964; but see Jeanne & Nordheim, 1996). Bees that feed on nectar and pollen from flowers, unless they can store honey and hibernate like honey bees, can only feed in summer in temperate climates. This limits their growing season and hence their colony size. The size of the nesting cavity (Wilson, 1959) and the nature of the nest-building materials (Hansell, 1987) may also constrain colony growth.

In short, mature colony size is likely to be determined, at least within broad limits, by a variety of conflicting ecological pressures. The main point of this section is to assert that, whatever the colony size settled upon in this process, certain social consequences follow (and these may in turn feed back and influence colony size themselves). This argument is developed in the following sections. In addition, it is possible that, over evolutionary time, there is an upward bias in the evolution of colony size. Colonies may tend to become larger within lineages because ecological niches for societies whose size exceeds the existing maximum are always vacant. This argument was made by Bonner (1988) for unitary organisms. As he put it, body size may increase over evolutionary time because 'there is always room at the top' (Bonner, 1988, pp. 58–59). In other words, the upper tail of the across-taxon distribution of mature body sizes may creep rightwards as lineages reach beyond the existing limit and, finding no competitors, remain there. By analogy, I suggest that the same argument could apply to colony size in social insects. If so, as Bonner (1988) argued for body design in unitary organisms, this could produce among social insect lineages a trend towards increasing social complexity over time.

### The social correlates of colony size

A survey of the properties of different taxa among the social insects (social Hymenoptera and termites) shows that colony size is associated with a suite of traits that together define the level of social complexity (Tables 1 and 2). These include the degree of morphological dimorphism between reproductives and workers (which from now on, for simplicity, I term *morphological skew*), the reproductive potential of workers (the degree to which workers are 'totipotent'), and the nature of the colony's life history (Table 1). Specifically, taxa with small colonies are characterized by a low degree of morphological skew and adult workers that have high reproductive potential. Taxa with large colonies exhibit a high degree of morphological skew and adult workers with low reproductive potential. Small societies are also more liable to have annual colony (life) cycles, whereas large ones are more liable to be perennial. Polymorphic workers are only found in large-colony species (ants and termites) (Table 1), as are the most elaborate communi-

**Table 1** Features of the major groups of eusocial insects in relation to colony size.

Group	Colony size to nearest order of magnitude	Degree of queen-worker caste dimorphism	Colony cycle	Queen replacement possible?	Worker polymorphism?	Totally sterile workers in some species?
<i>Small colonies:</i>						
Allodapine bees plus relatives (Xylocopinae)	10	None-low	Annual	Yes	No	No
Hover wasps (Stenogastrinae)	10	None-low	Annual, perennial	Yes	No	No
Sphecoid wasps (Pemphredoninae)	10	Very low	Annual, perennial	?	No	No
Bumble bees (Bombinae)	10–100	Medium	Annual	No	No	No
Independent-founding paper wasps (Polistinae)	10–100	None-low	Annual, perennial	Yes	No	No
Sweat bees (Halictinae)	10–100	None-medium	Annual, perennial	Yes	No	No
<i>Large colonies:</i>						
Yellowjackets and hornets (Vespinae)	10–1000	High	Annual	No	No	No
Swarm-founding paper wasps (Epiponini)	10–10 000	None-low	Perennial	Yes	No	No
Stingless bees (Meliponinae)	100–100 000	High	Perennial	No	No	Yes
Honey bees (Apini)	10 000–100 000	High	Perennial	No	No	No
Ants (Formicidae)	10–10 000 000	High	Perennial	No	Yes	Yes
Termites (Isoptera)	100–1000 000	High	Perennial	Yes	Yes	Yes

Modified from Bourke (1997), with additional information on worker polymorphism from Wilson (1971), on worker sterility in stingless bees from Inoue *et al.* (1994), and on queen replacement from: Plateaux-Quénu (1961), Wilson (1971), West-Eberhard (1978), Myles & Nutting (1988), Michener (1990a,b), Röseler & Van Honk (1990), Reeve (1991), Spradbery (1991) and Turillazzi (1991). Queen replacement in this context refers to the ability of adult individuals within the colony, who would otherwise be classified as workers, to replace the principal breeding female (or females) as resident sexual reproductives if she (or they) should die. Queen replacement in this sense is absent from ants except among some ponerines (Peeters, 1993; see text).

cation systems (Wilson, 1971; Michener, 1974; Breed, 1976; Jeanne, 1991) and nests (e.g. Jeanne, 1975; Wenzel, 1991). In sum, small societies tend to be simple (following the usage in the Introduction), and large ones to be complex. A connection of social complexity with colony size has previously been pointed out by several authors, for example Wilson (1971, pp. 181–182), Michener (1974, p. 47), Oster & Wilson (1978, pp. 196–197), Hölldobler & Wilson (1990, p. 160), Alexander *et al.* (1991), Tschinkel (1991) and Wheeler (1991).

It is likely that these across-taxon associations (Table 1) also hold within taxa that have a large range of colony sizes such as the swarm-founding polistine wasps, the

ants and the termites. For example, species of ponerine ants that lack morphological queens (species with reproduction by mated workers or 'gamergates') are exceptional among ants (Table 1) in exhibiting the functional equivalent of queen replacement (Peeters, 1993). These species also have, for ants, small colonies (Table 2). This suggests that the repeated transition among ponerines from species with morphological queens to 'queenless' species with reproduction by gamergates alone (Peeters, 1993), which represents a form of reversion in social evolution (cf. Wcislo & Danforth, 1997), was driven by ecological changes promoting reduced colony size. Among ants in general, Wilson (1971, p. 442) noted that

**Table 2** Evidence for associations of colony size with queen–worker caste dimorphism, reproductive potential of workers and worker polymorphism within social insect taxa.*1. Halictine bees*

(a) From a reanalysis of the data of Breed (1976) on *Lasioglossum* (*Dialictus*) bees, there was a significant, positive correlation between colony size and the degree of queen–worker size dimorphism (measured as the percentage size difference between queens and workers) across seven species and populations (Spearman's  $r = 0.81$ ,  $n = 7$ ,  $P < 0.05$ ).

(b) From a reanalysis of the data of Packer & Knerer (1985) on *Lasioglossum* (*Evyllaesus*) bees, there was a significant negative correlation between colony size and the percentage of mated workers per nest across 11 species and populations (Spearman's  $r = -0.74$ ,  $n = 11$ ,  $P < 0.01$ ). This suggests reduced selection for worker ability to replace queens, and to produce female progeny, as colony size rises. However, there were no significant correlations between colony size and either the degree of queen–worker size dimorphism (measured as relative wing length difference between queens and workers) (Spearman's  $r = 0.22$ ,  $n = 11$ ,  $P > 0.1$ ) or the percentage of ovary-developed workers (Spearman's  $r = -0.27$ ,  $n = 11$ ,  $P > 0.1$ ).

*2. Vespine wasps*

Analysis of data in Matsuura & Yamane (1990) showed that there was a significant positive association between colony size (number of cells) and the degree of queen–worker size dimorphism (queen to worker ratio of body lengths) in 14 species and subspecies of Japanese Vespinae (Spearman's  $r = 0.61$ ,  $n = 14$ ,  $P < 0.05$ ). However, this relationship was not significant if species for which there were only data on maximum colony sizes (as opposed to midrange colony sizes) were excluded (Spearman's  $r = 0.51$ ,  $n = 12$ ,  $0.1 > P > 0.05$ ).

*3. Swarm-founding polistine wasps*

From Fig. 1 of Jeanne (1980), a positive relationship exists between colony size and the degree of queen–worker size dimorphism (measured as the ratio of caste-specific body sizes) across 32 species (no statistical analysis was presented by the original author and none is possible from the published information).

*4. Ponerine ants*

(a) From a reanalysis of the data of Villet (1990) and Villet *et al.* (1991), monogynous species in which queens have more ovarioles per ovary than workers had greater colony sizes (median = 252 individuals,  $n = 10$  species) than species in which queens have the same number of ovarioles per ovary as workers (median = 83 individuals,  $n = 8$  species). However, this difference was not significant (two-tailed Mann–Whitney  $U$ -test,  $U_{10,8} = 57$ ,  $0.2 > P > 0.1$ ).

(b) From a reanalysis of the data of Peeters (1993), monogynous species with morphologically distinct queens ('dealate' or 'ergatoid' queens) had significantly larger colonies (median = 156 workers,  $n = 14$  species) than species lacking morphological queens ('gamergate'-only species) (median = 52 workers,  $n = 7$  species) (two-tailed Mann–Whitney  $U$ -test,  $U_{14,7} = 76$ ,  $P = 0.05$ ).

Only monogynous species were included in these two analyses, to control for possible differences in colony size due to differences in queen number. In the analysis of Peeters's (1993) data, only species in which the size of more than one colony was measured were included and species with dealate and ergatoid queens were pooled because their colony sizes were not significantly different (medians of 276 and 156 workers, respectively; two-tailed Mann–Whitney  $U$ -test,  $U_{8,6} = 25$ ,  $P > 0.2$ ). Peeters (1993, 1997) verbally recorded a link between small colony size and low queen fecundity (and, by extension, low morphological skew) in ponerine and other 'primitive' ants.

*5. Non-ponerine ants*

(a) Of 10 nonparasitic attine genera, eight have 'small', 'small to medium' or 'medium' mature colony sizes and monomorphic workers, and two have 'large' mature colony sizes and polymorphic workers (Hölldobler & Wilson, 1990, pp. 606–607).

(b) In 11 species of monogynous formicine and myrmicine ants in six genera, there was a significant negative relationship between colony size and the worker/queen thoracic size ratio, at both the species and subgeneric levels (species level: Spearman's  $r = -0.85$ ,  $n = 11$ ,  $P < 0.01$ ; subgeneric level: Spearman's  $r = -0.91$ ,  $n = 7$ ,  $P < 0.05$ ). Therefore, queens become relatively larger as colony size rises. Data on queen–worker size dimorphism were taken from Stille (1996), and on colony size from Bernard (1968), Collingwood (1979) and Seifert (1996).

*6. Termites*

Shellman-Reeve (1997) described an association between social type and colony size in termites. 'Single-site nesters' have maximum colony sizes of 600–8000 individuals, helpers and soldiers capable of becoming reproductive forms, and relatively unbranched individual developmental pathways (and hence low morphological skew). 'Multiple-site nesters' have maximum colony sizes of 10 000–1000 000 individuals, helpers that mostly abandon reproductive options in their development, sterile soldiers and highly branched developmental pathways (so permitting high morphological skew). Finally, 'central-site nesters' have up to 1–5 million individuals per colony, almost wholly sterile worker and soldier morphs and again highly branched developmental pathways. Shellman-Reeve (1997) attributed these associations to increasing resource stability across the social types. It is worth adding that resource stability most probably influences helpers' reproductive potential and morphological skew via its effects on colony size.

queens have more ovarioles per ovary as colony size rises, and this presumably reflects greater queen–worker differentiation. Examples of morphological skew, worker polymorphism and related traits increasing with colony size also exist within several other taxa (Table 2).

## The causal association between colony size, social complexity and the reproductive potential of workers

### Greater colony size leads to lower worker reproductive potential

Alexander *et al.* (1991) made the crucial point that colony size and two important elements of social

complexity, worker reproductive potential and morphological skew, are not just correlated; there is almost certainly a causal connection between them. Let queen replacement be defined as the ability of an adult worker to assume the queen's reproductive function should she die or be overthrown (Table 1). Alexander *et al.* (1991) argued that in a small colony any one worker has a comparatively high chance of replacing the queen, because it will have relatively few competitors. Therefore, there is selection for high reproductive potential among workers. This also promotes a lack of specialization for worker behaviour, and consequently low morphological skew. By contrast, Alexander *et al.* (1991) suggested that any one individual in a large colony has only a small chance of replacing the queen, because of the large number of competitors. This leads to selection for low reproductive potential, greater specialization in the worker role and high morphological skew. For example, worker ants are so specialized in their role that they have lost their wings and (usually) some or all of their reproductive apparatus. Consequently, they have also lost their ability either to replace the queen or to disperse far and act as queens elsewhere. As adults, they are effectively 'trapped' into social life (West-Eberhard, 1975).

It is useful to add to the argument of Alexander *et al.* (1991) in a way not considered by these authors. This is by examining the effect of colony size on the workers' propensity to assume the queen's reproductive role during the queen's lifetime. The question is whether a worker should attempt to replace a queen-laid egg with a worker-laid egg (either one of her own or one belonging to another worker). This decision was analysed by Ratnieks (1988) in the context of the evolution of *worker policing* (mutual prevention by workers of one another's reproduction) in the case of a matrilineal (mother-daughter) haplodiploid society with a single queen who may be singly or multiply mated (see also Ratnieks, 1990; Ratnieks & Reeve, 1992). In the Hymenoptera, haplodiploidy implies that unmated females, including workers, may retain the ability to lay unfertilized, haploid (male) eggs. Ratnieks (1988) showed that worker policing of male-production by workers should evolve when the effective mating frequency of queens exceeds two (from here on, I use 'mating frequency' alone as shorthand for effective mating frequency). For, in this case, workers are more closely related to the average queen-produced male (a brother,  $r = 0.25$ ) than to the average worker-produced male (a nephew or the son of a half-sister, average  $r < 0.25$ ). As a result, a policing gene for mutual inhibition of worker male-production (so resulting in the rearing of brothers) could invade a nonpolicing population. Note that, critically, this argument relies on no single worker being able to dominate worker male-production. If such domination were possible, a laying worker would always be selected to raise sons ( $r = 0.5$ ) over any other type of male. For this

reason, Ratnieks (1990) and Ratnieks & Reeve (1992) suggested that worker policing might be ineffective in small colonies.

Extending this logic, it is evident that colony size alone affects the evolution of worker policing, independently of mating frequency. The crucial point is that, as colony size increases, a worker's proportionate representation among worker-laid eggs falls because it becomes increasingly difficult for a single worker to dominate worker reproduction. In a small colony, a single worker can reasonably aim to monopolize worker reproduction because there are few competitors for it to dominate. But in a large colony, no single worker could produce all the worker-derived offspring, because it would have too many competitors to dominate. Consequently, in a small colony, a worker faces the decision whether to replace a queen-laid egg with one of its own. In a large colony, the decision is whether to replace a queen-laid egg with one from some other worker, since the average worker-produced offspring will no longer be its own (setting aside the negligible fraction of eggs produced by the focal worker itself). Put another way, a rise in colony size is associated, almost inevitably, with a fall in the power of any one individual worker relative to the collective of workers.

I applied this argument to determine the effect of colony size on the evolution of worker policing in different types of social group. All groups had two generations with subordinates (workers or helpers) belonging to the offspring generation (Tables 3–5; see also Ratnieks, 1990), since this is a very widespread social structure. The results showed that, with a few important exceptions, worker reproduction is selected in small colonies, whereas it is easier for worker policing to invade in large colonies. This applies in both diploids and haplodiploids, with either single or multiple breeding females, and at high or low mating frequencies (Tables 3–5). The essential reason why rising colony size promotes worker policing is that it makes the average worker-produced offspring shift from being a focal worker's own progeny to being the less closely related offspring of another worker. This increases the inclusive fitness gain from policing relative to that obtained from rearing worker-produced offspring.

The exceptions to the above argument occur mostly under haplodiploidy, and are due to the relatedness asymmetries inherent to this genetic system (Ratnieks, 1988, 1990; Pamilo, 1991b). For example, a key exception occurs in social Hymenoptera with single queens (monogyny). In large colonies under single mating, workers are more closely related to worker-produced males (nephews,  $r = 0.375$ ) than to queen-produced ones (brothers,  $r = 0.25$ ). Worker policing of one another's male production is only expected in large colonies at mating frequencies greater than two (Ratnieks, 1988; Table 5). In addition, worker policing of male production is expected to occur under fewer

**Table 3** Relatedness values in diploid and haplodiploid social groups.

	Relatedness of worker to offspring of given type and sex	
	Female	Male
<i>Diploids</i>		
Queen offspring	$[1 + 1/k + (N - 1)G]/4N$	$[1 + 1/k + (N - 1)G]/4N$
Own offspring	$\frac{1}{2}$	$\frac{1}{2}$
Other worker's offspring	$[1 + 1/k + (N - 1)G]/8N$	$[1 + 1/k + (N - 1)G]/8N$
<i>Haplodiploids</i>		
Queen offspring	$[1 + 2/k + (N - 1)G]/4N$	$[1 + (N - 1)G]/4N$
Own offspring	$\frac{1}{2}$	$\frac{1}{2}$
Other worker's offspring	$[1 + 2/k + (N - 1)G]/8N$	$[1 + 2/k + (N - 1)G]/8N$

The table shows life-for-life relatednesses (Grafen, 1986) between a female focal worker (helper) in the offspring generation and various categories of potential progeny within the group. The group has  $N$  equally reproductive females in the parental generation (queens), each mated with  $k$  males. The life-for-life relatedness between the breeding females is  $G$ . The tabulated relatedness values are calculated as the average of the relatednesses of a focal worker to each class of offspring of the given type and sex, weighted by the frequencies of these classes (Pamilo, 1991b). Setting  $N = 1$  and  $k = 1$  gives the relatedness values for the case when there is one queen per social group (monogyny), who is singly mated. For example, under monogyny and monandry in haplodiploids, a focal worker is related to a female offspring of the queen by 0.75 (sister), to her own female offspring by 0.5 (daughter) and to a female offspring of another worker by 0.375 (niece).

combinations of colony size and mating frequency than worker policing of female production (Table 5). This could help explain why workers in social Hymenoptera frequently retain their ovaries but not their sperm receptacles (a reproductive system that confers the ability to produce males but not females) (cf. Ratnieks, 1988). However, a capacity for personal reproduction via male production is, in the Hymenoptera, less of a barrier to morphological specialization as a worker (increased morphological skew) than the capacity for personal reproduction via female production. This is because only female production requires morphological adaptations for finding and securing a mate. This helps explain how high morphological skew can coexist with the substantial levels of worker male-production found in some 'advanced' social Hymenoptera (Bourke, 1988; Ratnieks, 1988). Note also that workers are expected to favour producing worker-derived females in small colonies at mating frequencies greater than two (Table 5) (since a focal worker is then more closely related to its own daughters,  $r = 0.5$ , than to those of the queen,  $r < 0.5$ ). This predicts that worker retention of the sperm receptacle should be disproportionately likely in monogynous species with small colonies and multiply mated queens, as opposed to monogynous species with large colonies or with small colonies and singly mated queens.

Overall, these findings imply that, in the queen's lifetime, specialization for worker behaviour should be stronger in larger colonies. This specialization is also likely to hamper efficient queen replacement, so augmenting the negative effect, already described, that large colony size has on the evolution of the ability of workers to replace dead queens (Alexander *et al.*, 1991). The conclusion is that, through its effect on both queen replacement and worker policing, large colony size encourages the loss of reproductive potential among

workers. This in turn allows the evolution of higher morphological skew.

#### Feedback between greater colony size, loss of worker reproductive potential and rising morphological skew

There are several ways in which changes in colony size, worker reproductive potential and morphological skew are bound together by feedback loops of mutual reinforcement. To begin with, the promotion by large colony size of worker policing could be self-reinforcing via its influence on colony productivity. Worker policing is likely to permit colony productivity to increase, as workers not engaged in reproduction are more able to undertake tasks beneficial to the colony (Ratnieks, 1988). Rising productivity could entail the production of a larger

**Table 4** Worker policing in diploid social groups.

	Effective mating frequency ( $k = 1$ )	Effective mating frequency ( $k > 1$ )
<i>Single queen case (<math>N = 1</math>)</i>		
Small colony (either sex)	$r_{\text{WORKER}} = r_{\text{QUEEN}}$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Large colony (either sex)	$r_{\text{QUEEN}} > r_{\text{WORKER}}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$
<i>Multiple queen case (<math>N &gt; 1</math>)</i>		
Small colony (either sex)	$r_{\text{WORKER}} > r_{\text{QUEEN}}$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Large colony (either sex)	$r_{\text{QUEEN}} > r_{\text{WORKER}}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$

Worker policing is selected if  $r_{\text{QUEEN}} > r_{\text{WORKER}}$ , i.e. if a focal worker's relatedness to the queen's offspring exceeds its relatedness with same-sex worker-produced offspring. Correspondingly, worker reproduction is favoured if  $r_{\text{WORKER}} > r_{\text{QUEEN}}$ . In a small colony,  $r_{\text{WORKER}}$  = a focal worker's relatedness to its own offspring, whereas in a large colony it equals its relatedness to the offspring of other workers (see text). The inequalities are obtained by comparing the relatedness values in Table 3 for given  $k$  and  $N$  values.

workforce, and this would then enhance selection for worker policing. On top of this, rising morphological skew involves, in a complementary fashion, both increasing specialization of queens as reproductive aid-receivers and increasing specialization of workers as aid-givers (West-Eberhard, 1975). The associated rise in the relative fecundity of queens and productivity of workers again permits a rise in colony size, as both these changes allow more workers to be reared. Moreover, as colony size and morphological skew increase, there is the possibility for absolute worker body size to fall. This would allow more workers to be produced for the same resources and colony size to increase yet more. Oster & Wilson (1978, p. 102) noted a tentative association between small body size and the lack of ovaries in worker ants; from the current paper's perspective, this association is predicted to be mediated by increased colony size.

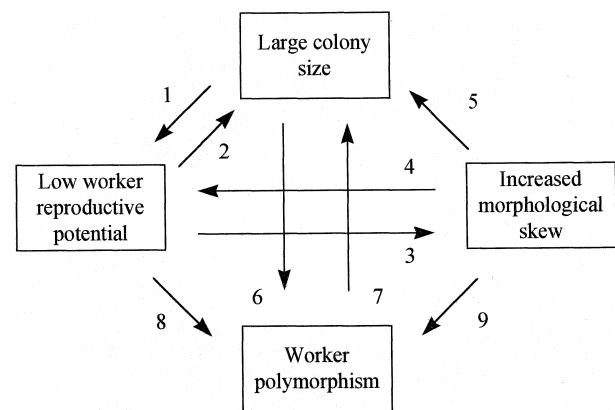
Another factor is that as workers become more specialized in their roles (with rising morphological skew), there is selection for the lifespans of reproductives and workers to diverge (Alexander *et al.*, 1991; Keller & Genoud, 1997). In support of this, surveys of longevity data find that queens live 'much longer' than workers in ants (Hölldobler & Wilson, 1990, p. 168). One reason for divergent queen and worker lifespans is that senescence affects reproductives later than workers, since reproductives typically produce sexuals after a phase of worker-production, whereas workers can start to rear the reproductives' brood as soon as they are physically capable. A second reason is that reproductives, being sheltered in the nest, experience lower rates of extrinsic mortality than workers, which perform risky foraging tasks (Alexander *et al.*, 1991; Keller & Genoud, 1997). If workers senesce early through helping, then reproduction later in life is correspondingly less valuable to them (Alexander *et al.*, 1991), and worker specialization can proceed yet further. Furthermore, as worker lifespans fall relative to those of queens, the opportunity for a worker to replace a dead queen must also diminish through a reduction in the temporal probability of the queen requiring replacement (Alexander *et al.*, 1991). This is because the queen is unlikely to die during the entire lifetime of an average worker. Consequently, specialization as a worker can again increase.

Finally, if large colonies experience queen replacement relatively rarely (due to long-lived queens and short-lived helpers unsuited to rapid and efficient queen replacement), the long-term stability and predictability of their kin structures will also be comparatively higher than those of small colonies (F. L. W. Ratnieks, personal communication). For example, some ant colonies are estimated to retain the same single queen for 20 years in the field (Pamilo, 1991c). Such long-term stability will make opting for a worker phenotype a comparatively risk-free option in a large as opposed to a small colony (because the chance of rearing a brood less closely related to oneself than those reared initially, due to an unfore-

seen queen replacement, is lower). The conclusion is that small colony size, high worker reproductive potential and low morphological skew coevolve to form one set of mutually stable traits, whereas large colony size, low worker reproductive potential and high morphological skew coevolve to form another (Fig. 1).

### Causal associations of colony size with colony life history, worker polymorphism, the communication system and nest type

As well as promoting higher morphological skew, increasing colony size is causally linked to other aspects of social complexity. The first is the nature of the colony's life history. Simply, annual colonies tend to be small because they have little time to grow, whereas perenniality is associated with large colony size because perennial colonies, by definition, can grow over many years. The second size-linked feature is worker polymorphism. Small societies, being less insulated against environmental challenges, require workers that are relatively plastic in the roles they can adopt. However, large societies, being relatively buffered against outside factors, can take advantage of the more efficient division of labour that stems from having physical worker castes (Sudd & Franks, 1987, p. 73; Bonner, 1988, p. 216; Wheeler, 1991). This argument is analogous with one put forward regarding the effects of increased body size in unitary



**Fig. 1** Summary of the effects of large colony size on worker reproductive potential, morphological skew and worker polymorphism. Numbered arrows show causal links and feedback loops. They represent effects due to the proposed influence of (1) colony size on queen replacement and worker policing, (2) policing on colony productivity, (3) nonreproductive worker specialization on morphological skew, (4) morphological skew on divergence of queen and worker lifespans, (5) morphological skew on queen and worker productivity, (6) colony size on optimal system of division of labour, (7) worker polymorphism on colony efficiency and hence colony size, (8) worker reproductive potential on permissible worker morphologies and (9) morphological skew on the timing of caste determination and hence degree of worker polymorphism.

organisms. In these, it has been argued that greater body size involves a greater number of types of cell and tissue through the need for a higher degree of division of labour (Haldane, 1927; Bonner, 1988, p. 161; Bell & Mooers, 1997). In social insects, the enhanced colony efficiency brought about by worker polymorphism may, in another case of positive feedback, increase colony productivity and hence itself act as a promoter of large colony size. Large colony size also promotes worker polymorphism by favouring a lower reproductive potential among workers. This is because nonreproductive workers are more likely to evolve the specialized body morphologies associated with physical worker castes (Oster & Wilson, 1978, p. 102). They are especially likely to evolve soldier morphology, because being a soldier designed for colony defence is risky (Passera *et al.*, 1996). Furthermore, high morphological skew may itself facilitate worker polymorphism, because early queen-worker caste determination makes the whole of the workers' developmental period available for the generation of alternative worker morphologies (Wheeler, 1986; Fig. 1).

A third consequence of large colony size is the elaboration of the communication system. Large colonies presuppose more elaborate modes of communication among the workers both because there are more kinds of tasks to perform and because information must be conveyed to more partners over greater distances. One example is the rising complexity of routes by which materials and information are transferred between individuals as colony size grows in bees (Michener, 1974, pp. 193–196). Another is the change in the foraging and recruitment system from an individual-based system to one involving mass communication as colony size rises in ants (Beckers *et al.*, 1989). Finally, colonies that are large, perennial or both are also more permanent, and this allows them to have more elaborate nests.

### **Colony size and the nature of within-colony reproductive conflict**

#### **Conflict over worker reproduction and queen replacement vs. conflict over brood composition**

The previous sections have argued that colony size influences the degree to which workers retain their reproductive potential. A corollary of this reasoning is that colony size also affects the nature of queen-worker reproductive conflict within the society. Such conflict may occur directly over reproduction, or indirectly over brood composition. Prime examples of this second type of conflict are evolutionary disagreement over sex allocation (Trivers & Hare, 1976) and queen:worker caste ratios (Pamilo, 1991a). In small societies, where queen replacement and worker reproduction are strongly selected, subordinates should constantly threaten the queen reproductively. In addition, owing to the low morphological skew prevailing in small societies, subordinates

should be relatively capable, in physical terms, of challenging the queen. These factors should make the queen continually active in maintaining her dominant breeding position (Alexander *et al.*, 1991; Sherman *et al.*, 1995). Put another way, queen policing of worker reproduction should be strongest in small societies. A further reason for this is that small societies are easiest for a single queen to dominate (Ratnieks, 1988). Therefore, in small societies, workers are most strongly selected to be reproductive and, simultaneously, queens are most able to hinder them. This should lead to intense, direct conflict over reproduction.

In large societies, where workers are not strongly selected to be prepared for queen replacement or to reproduce, and are physically less capable of challenging the queen, conflict will tend not to be over the identity of the breeding individual but over brood composition alone. This contrasts with the view (e.g. Oster & Wilson, 1978, p. 103) that species with the largest colonies should have the most reproductive workers because of the difficulty of queen policing in a large colony. Conflict over queen succession may occur in large colonies if the current queen weakens or dies, but it will then tend to be over what new queen to accept as the successor (where the social system permits), not among adult workers to replace the queen.

#### **Colony size, the timing of queen-worker caste determination, and the manipulation of caste membership**

Workers in small societies, with their high chance of being replacement queens, should be selected to keep their reproductive options comparatively open at each stage in their lives, in case changing circumstances permit them a reproductive opportunity. Therefore, they should opt for caste determination late in their lives, if at all. Queens, by contrast, would be favoured who manipulated subordinates into becoming workers relatively early, as this would reduce future challenges to the queens' reproductive dominance. In contrast, individuals in large societies, with little chance of being replacement queens, have comparatively no bar to early caste determination. Indeed, selection for specialization as workers will favour early caste determination. This is because early determination is necessary to achieve high morphological skew, since events happening earlier in development will have a greater influence on final form (Michener, 1974, p. 95; Wheeler, 1986). Queens would still favour earlier caste determination among workers, but in this case to promote greater colony efficiency. For these reasons, small societies should be associated with late queen-worker caste determination (or none at all) and individuals relatively resistant to manipulation of their caste, and large societies should exhibit early caste determination and individuals relatively compliant to manipulation of their caste (Alexander *et al.*, 1991). In



some ant species with single queens, queen replacement by individuals within the colony is totally precluded by the mating system (mating occurs in a swarm far from the colony) (Bourke & Franks, 1995, p. 228). In such species, where a female larva's chance of being a replacement queen is nil, early worker determination should be favoured all the more strongly.

The extent to which queens directly influence caste in social insects is a poorly understood topic. The suggestion that queens manipulate individuals into being workers is an old one (Alexander, 1974; Michener & Brothers, 1974; West-Eberhard, 1975). One way in which such parental manipulation might occur would be for queens to underfeed their offspring and so make them 'subfertile' (Craig, 1983). A possible example is found in the polistine wasp, *Ropalidia marginata*, in which females fed less as larvae are less likely to become egg-layers. In other words, there is preimaginal caste determination in a species lacking morphological queens (Gadagkar *et al.*, 1988, 1990, 1991). In ants, the presence of queens also influences caste (Hölldobler & Wilson, 1990, p. 348). However, female larvae opting to be workers in the presence of the queen could be doing so not through manipulation by the queen, but as a self-interested response to signals provided by her (Keller & Nonacs, 1993; Keller & Reeve, 1994). This is especially likely to be true from the viewpoint of the current paper, as ants tend to be large-colony species.

## Discussion

### Colony size, social complexity and kin structure

The main argument of this paper is that, once mature colony size in social insects is set by ecological factors, there are a number of important consequences for social organization. Specifically, colony size is a major determinant of the reproductive potential of workers and the level of morphological skew between reproductives and workers. These factors may in turn influence colony size in a process of positive feedback. It is important to appreciate that this perspective does not rule out an influence of other factors on social complexity. Foremost among these is the kin structure of the society, which undoubtedly has far-reaching effects on the expected reproductive behaviour of workers (Hamilton, 1964; Trivers & Hare, 1976; Ratnieks & Reeve, 1992). Note, however, that societies may have fairly similar kin structures while differing greatly in their complexity. For example, *Xylocopa sulcatipes* carpenter bee societies (Stark, 1992) and *Melipona* stingless bee societies (Engels & Imperatriz-Fonseca, 1990) both consist of single, once-mated queens plus their daughter offspring. But the carpenter bee colonies contain two individuals only and are simple, whereas the stingless bee colonies contain many thousands of individuals and are complex. Therefore, although the most complex societies tend to be

those with single queens (West-Eberhard, 1982), kin structure alone does not account for social complexity. Colony size is a far better correlate. On the other hand, one way of viewing the predicted effect of colony size on queen replacement and worker policing (Tables 3–5) is to regard colony size as altering the kin-selected interests of workers so as to make them resemble more those of queens (by making workers less prone to replace the queen and more prone to rear her offspring). In other words, greater colony size leads to an increasing coincidence of interest among the two parties (Ratnieks & Reeve, 1992; Bourke & Franks, 1995). In this sense, the effect of colony size is intimately connected with kin structure.

### Colony size, social complexity and reproductive skew

Reproductive skew refers to the degree of sharing of reproduction among nestmates (e.g. Keller & Reeve, 1994). The transition from simple to complex societies appears associated with an increase in reproductive skew (Keller & Reeve, 1994; Sherman *et al.*, 1995). From the viewpoint of the present paper, this occurs because large and complex societies combine the highest morphological skew with the greatest number of nonreproductive members, which by definition means that most reproduction will be concentrated in relatively few, specialized individuals. Sherman *et al.* (1995) also pointed out a positive association between reproductive skew and colony size (characterized as a rightwards shift along their 'eusociality continuum'), and explained it in essentially the same way. However, the link of reproductive skew and colony size is not well recognized in existing formal indices of skew. Reeve and Keller's skew index (Keller & Vargo, 1993; Reeve & Ratnieks, 1993)

**Table 5** Worker policing in haplodiploid social groups.

	Effective mating frequency ( $k$ ) < 2	Effective mating frequency ( $k$ ) > 2
<i>Single queen case</i> ( $N = 1$ )		
Small colony (female)	$r_{\text{QUEEN}} > r_{\text{WORKER}}$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Small colony (male)	$r_{\text{WORKER}} > r_{\text{QUEEN}}$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Large colony (female)	$r_{\text{QUEEN}} > r_{\text{WORKER}}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$
Large colony (male)	$r_{\text{WORKER}} > r_{\text{QUEEN}}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$
<i>Multiple queen case</i> ( $N > 1$ )		
Small colony (female)	$r_{\text{QUEEN}} > r_{\text{WORKER}}^*$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Small colony (male)	$r_{\text{WORKER}} > r_{\text{QUEEN}}$	$r_{\text{WORKER}} > r_{\text{QUEEN}}$
Large colony (female)	$r_{\text{QUEEN}} > r_{\text{WORKER}}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$
Large colony (male)	$r_{\text{WORKER}} > r_{\text{QUEEN}}^{**}$	$r_{\text{QUEEN}} > r_{\text{WORKER}}$

See first part of legend for Table 4. \*Inequality holds if  $N < (1 + 2/k - G)/(2 - G)$ . \*\*Inequality holds if  $N < 1 + (2/k - 1)/G$ . Worker reproduction is always favoured in small groups, except in the female progeny case when  $k < 2$  (in multiple queen groups, only for some values of  $N$ ,  $k$  and  $G$ ). Worker policing is always favoured in large groups, except in the male progeny case when  $k < 2$  (in multiple queen groups, only for some values of  $N$ ,  $k$  and  $G$ ).

and Pamilo & Crozier's (1996) skew index are both invariant (each equalling 1) for the case of a single reproductive queen plus sterile worker daughters, regardless of worker number. (On the other hand, Keller & Perrin's (1995) eusociality index rises with increasing worker number in this example.) In addition, reproduction by just a single individual (i.e. a skew of 1 according to the formal indices) is not inevitably linked to colony size or to social complexity. This can be seen by considering again the comparison of carpenter bees with stingless bees, or by comparing polistine with vespine wasps (Ross & Matthews, 1991). Societies in both groups within each taxon (bee or wasp) often have a single reproductive queen, but still differ greatly in size and complexity.

### Extension to other social taxa

The interest in comparing vertebrate and invertebrate societies, already present in the earlier literature (e.g. Alexander, 1974; Wilson, 1975), has recently been increasing (Alexander *et al.*, 1991; Crespi & Yanega, 1995; Sherman *et al.*, 1995; Brockmann, 1997). A clear implication of the arguments in the present paper is that the size of social groups should affect the degree of social complexity, the propensity of helpers to reproduce and the nature of within-group conflict in vertebrates in exactly the same way as in insects. In fact, a social resemblance of small-colony forms of social insects and cooperatively breeding vertebrates was highlighted by Alexander *et al.* (1991) and Sherman *et al.* (1995). From this, it follows that vertebrate societies never attain the level of complexity of insect societies because they fail to grow as populous. It therefore becomes interesting to ask why vertebrate societies are held down at smaller sizes than invertebrate ones. Possible reasons include a limit to the expandability of nest sites among vertebrates (Alexander *et al.*, 1991), limits to their clutch and litter sizes (stemming from their larger body sizes), the possibility for long-lived individuals to become temporarily nonreproductive 'floaters' (Koenig *et al.*, 1992) in an ecologically constrained population rather than helpers, and limits to cognitive processing power in species such as primates whose sociality is based partly on reciprocity and alliance formation (Dunbar, 1992).

In support of these arguments, the social vertebrate with the largest average group size, the naked mole-rat (*Heterocephalus glaber*), has – as expected – the most complex societies. In this species, average group size, which is related to the species' ecology (Faulkes *et al.*, 1997), is 70–80 individuals and the maximum is nearly 300 individuals (Jarvis *et al.*, 1994). Furthermore, the naked mole-rat exhibits the closest approximation in vertebrates to appreciable morphological skew. This is shown by the fact that the breeding female develops elongated vertebrae (associated with greater body size and reproductive capacity) (Jarvis *et al.*, 1991) and by the

existence of a morphologically distinct disperser form among males (O'Riain *et al.*, 1996). In addition, the lifespans of queen and worker naked mole-rats are believed to be notably divergent (Jarvis *et al.*, 1994). This implies that, although queen replacement can occur (e.g. Clarke & Faulkes, 1997), the average worker remains under a single queen in its lifetime. Finally, unusually among cooperatively breeding mammals, naked mole-rats exhibit physiological blocks to reproduction in nonbreeders of both sexes, not just among females (Faulkes & Abbott, 1997). This further suggests a high degree of worker specialization.

### Conclusions and predictions

This paper's chief conclusion is that colony size alone explains a large amount of social diversity, and in principle it does so across all social taxa. Several predictions follow, which deserve testing in future research. First, small societies should never be complex (e.g. show high morphological skew). Second, the associations between various traits and colony size that occur across and, in the cases examined, within social insect taxa (Tables 1 and 2) should also occur within other social insects and across and within other taxa of social species. Third, in social insects, determination as a member of the worker caste is likely to be comparatively voluntary in large-colony species, especially in those where the social and mating system precludes queen replacement. For example, 'blastogenic' (in the egg) caste determination should be more likely to occur in ants that either have large colonies, or lack queen replacement, or both. Fourth, in all social taxa, the absence of reproduction by workers (helpers) in large groups should not necessarily be taken as evidence of reproductive suppression by a dominant; it could instead stem from mutual inhibition among workers of one another's reproduction (policing). However, one might not always expect workers even to attempt to reproduce in large groups (and then to fail through mutual policing), because the beneficial effects of policing on group productivity may lead to a self-imposed failure to reproduce (self-policing: Ratnieks, 1988). The preferential occurrence of either mutual policing or self-policing in large groups would also support the prediction of Keller & Nonacs (1993) that the degree to which pheromones emitted by reproductives which suppress potential replacements are coercive rather than communicative will fall with rising colony size.

Finally, at a more general level, the perspective in this paper suggests that the emergence of individuality (Buss, 1987; Michod, 1996, 1997) in evolutionary transitions involving changes in the way genetic information is transmitted (Maynard Smith & Szathmáry, 1995) could be facilitated by an increase in group size *per se*. In sum, recognizing the full effect of colony size on the extraordinary transition from simplicity to complexity among insect societies leads to an enriched understanding of

social diversity in insects, helps integrate yet further the study of social evolution in invertebrates and vertebrates, and could provide insights into the evolution of individuality at other levels of biological organization.

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