Relatedness and the fraternal major transitions

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Many of the major transitions in evolution involved the coalescence of independent lower-level units into a higher organismal level. This paper examines the role of kinship, focusing on the transitions to multi-cellularity in animals and to coloniality in insects. In both, kin selection based on high relatedness permitted cooperation and a reproductive division of labour. The higher relatedness of haplodiploid females to their sisters than to their offspring might not have been crucial in the origin of insect societies, and the transition to multicellularity shows that such special relationships are not required. When multi-cellular forms develop from a single cell, selfish conflict is minimal because each selfish mutant obtains only one generation of within-individual advantage in a chimaera. Conditionally expressed traits are particularly immune to within-individual selfishness because such mutations are rarely expressed in chimaeras. Such conditionally expressed altruism genes lead easily to the evolution of the soma, and the germ line might simply be what is left over. In most social insects, differences in relatedness ensure that there will be potential conflicts. Power asymmetries sometimes lead to such decisive settlements of conflicts that social insect colonies can be considered to be fully organismal.

Keywords: major transitions; kin selection; multicellularity; social insects; conflicts of interest

1. INTRODUCTION

When we look at how organisms interact, cooperation and altruism seem comparatively rare. The norm seems to be selfish competition, social insects and a few other organisms notwithstanding. However, this conclusion holds only because we normally confine our attention to the airy spaces that separate present-day organisms. A different picture is revealed once we dip into the watery realms beneath the skins, integuments and membranes of these same organisms. Here, all seems cooperative: the organs of the body, the organelles of the cell, the genes within the nucleus all seem bent towards a common goal, namely the survival and reproduction of the organism in which they reside. This seems so natural that it is rarely questioned; What else would one expect of a process of natural selection working on individual organisms? If we confine our attention to individual organisms, adaptation requires no special explanation beyond that provided by Charles Darwin: natural selection and adaptation.

However, organismal organization does require special explanation. It does not extend back to the dawn of life in an unbroken chain of inwardly selfless and outwardly selfish behaviour. Instead, the inward–outward boundaries have been altered, and units that were formerly competitive have come together in new cooperative, organismal entities. These events are perhaps the most salient of Maynard Smith & Szathmáry's (1995) major transitions of evolution. Replicating molecules came together in compartments, replicators linked together into chromosomes, separate prokaryotic species combined to found the eukaryotes, sexes pooled their genetic material, cells multiplied into multicellular organisms, and indivi-

duals coalesced into colonies. Each of these signal events in the history of life required potentially independent replicators to merge their own individual reproductive interests into the larger reproductive agenda of a new kind of organism. Life, at the crucial level of the organism, is cooperative. The history of how this has happened, though still imperfectly worked out, must surely be one of the great stories of biology.

One of the tasks, and pleasures, now facing us is to put together the full picture of these major transitions. Now that we realize that many share the common feature of forging a new cooperative unit, we can make comparisons from one level to another. In what ways was the evolution of cooperation different and in what ways was it similar? In an earlier paper I found it useful to pose the choices in terms of the rallying cry of the French revolution: *liberté, fraternité, egalité* (Queller 1997). Liberty is the course that most organisms follow most of the time, each going its own way. However, on rare occasions, a major transition can occur that results in alliances that are either fraternal or egalitarian, or both. Table 1 shows some of the characteristics of these two types.

Some alliances are egalitarian in the sense that all the participants retain reproductive rights. This is often necessary because the participants are very different from the beginning, with each contributing distinct functions that only it can perform and transmit. For example, the incorporation of the symbiotic bacteria that became mito-chondria resulted in an egalitarian alliance in which host and symbiont performed different functions, presumably from the very beginning.

In contrast, fraternal alliances such as the colonies of social insects were initially composed of similar, related

Table 1. *Two kinds of major transition*

(From Queller (1997).)

	egalitarian	fraternal
examples of cooperative alliances forged	different molecules in compartments; genes in chromosomes; nucleus and organelles in cells; individuals in sexual unions	same molecules in compartments; same organelles in cells; cells in individuals; individuals in colonies
units	unlike, non-fungible	like, fungible
reproductive division of labour	no	yes
control of conflicts	fairness in reproduction; mutual dependence	kinship
initial advantage	division of labour; combination of functions	economies of scale; later division of labour
means of increase in complexity	symbiosis	epigenesis
greatest hurdle	control of conflicts	initial advantage

units. Division of labour evolved later through epigenesis, with a common programme being expressed differently in different units. Because there is a common programme, a reproductive division of labour can evolve, with some units becoming sterile helpers.

In this paper I shall focus on the role of relatedness in the fraternal major transitions. In particular I compare the two transitions that are highest up in the hierarchy of life: the transitions from single-celled organisms to multicellular ones, and the transition from individuals to colonies. The other fraternal transitions listed in table 1 are also worthy of attention, but I shall ignore them here for two reasons: first, the histories of these two transitions are buried more deeply in the past, so less is known about them, and second, they seem to be fraternal parts of transitions that are more fundamentally of the egalitarian type. When replicating molecules were compartmentalized, molecules of the same type bore a fraternal kind of relationship to each other, but the chief importance of the event was the compartmentalization of molecules of different types, performing different functions. The same can be said of fraternal cooperation between organelles such as mitochondria, whose main importance lies in their egalitarian symbiosis with the host cell.

Even within the narrower scope of the transitions to multicellular individuals and to colonies, my account will be incomplete. Because they are what we know best, I shall primarily use social insects as exemplars of the transition from individual to colony, aware that I am giving short shrift to other colonial organisms. Similarly, when I discuss multicellularity, I shall usually have in mind metazoan development from a single cell.

2. RELATEDNESS

(a) *Hamilton's rule*

The key feature defining the fraternal major transitions is, of course, genetic relatedness. To the extent that two individuals are related, they can transmit each other's programmes. An individual can even altruistically forgo reproduction if by so doing it sufficiently increases the reproduction of relatives who share the same genes. Hamilton's rule (Hamilton 1964*a*,*b*) specifies the conditions that must be met: $br_b > cr_c$. Here, b is the fitness gain to the beneficiary of the altruism and c is the fitness cost to the altruist, and the r_b and r_c variables are the relatednesses of the altruist to the two parties (or to their offspring). Relatedness measures the extent to which an allele found in one individual (here the altruist) is found, above random expectation, in another individual. It therefore defines the altruist's genetic exchange rate appropriate for fitness transfers to the beneficiary.

The beauty of Hamilton's rule is that it squeezes a great deal of ugly population genetics into a few simple variables. To do so, a few assumptions needed to be met (Seger 1981; Michod 1982; Grafen 1985; Queller 1992). The most important assumption for explaining the evolution of sterility of social castes, the most extreme form of altruism, concerns conditionality. Unconditional sterility of an altruist cannot evolve, no matter how high the relatedness, because the altruistic alleles always remove themselves in favour of the non-altruistic alleles. Instead, the expression of sterility genes must be conditioned on some environmental cue, such that those who express the sterility benefit others who do not express it, but do transmit it (Charlesworth 1980; Parker 1989).

(b) *Unitary and aggregate development*

Relatedness has such a simple role in the transition to multicellularity that for a long time it received little attention. When the multicellular form develops from a single cell undergoing mitotic divisions, which I shall call unitary development, it is a clone of genetically identical cells (except for new mutations, which will be discussed in § 3). Because $r_b = r_c$, some of these cells can become sterile somatic tissues in the service of the other cells if this increases the total reproduction of the group of cells, i.e. if $b > c$. The high relatedness that results with unitary development from a single cell might help to explain why this mode of development is so common (Maynard Smith 1989; Grosberg & Strathmann 1998), although other factors might include the purging of deleterious mutations, the enhanced dispersal of small propagules and the fact the product of sex is typically a single cell.

To understand better the importance of relatedness, more attention needs to be paid to those organisms that develop in non-standard ways, such as by the aggregation of formerly separate cells. A well-known example is the cellular slime moulds such as *Dictyostelium discoideum* (Bonner 1967; Raper 1984). These organisms normally live as single-celled predatory amoebae, but when their food runs out they undergo a remarkable transformation.

The starving cells both send out and follow chemical signals, resulting in large aggregations of cells. These aggregations then differentiate, without further cell division, into a sterile stalk and one or more heads of fertile spores. Because the multicellular stage is formed by an aggregation of cells that could be genetically different, two results follow that could be detrimental to the evolution of organismal cooperation (Buss 1982; Armstrong 1984; DeAngelo *et al.* 1990; Matsuda & Harada 1990; Gadagkar & Bonner 1994). First, relatedness might be lowered so that Hamilton's rule is harder to satisfy. Of course, if relatedness is not too low and the benefit:cost ratio is sufficiently high, this is not necessarily a problem. Second, even if Hamilton's rule is satisfied, such that average relatedness is high enough to support co-operation, there might still be selection to cheat. The best outcome for a particular genotype that finds itself in a chimaeric mixture would be to differentiate entirely into spore cells, provided that the other genotypes formed an adequate stalk. Buss (1982) described a natural stalkless strain that does just that. More recent work shows that *D. discoideum* clones mix freely and that cheating is common in mixtures (Strassmann *et al.* 2000).

(c) *Social insects*

The role of relatedness in social insects resembles in some respects its role in unitary development, and in other respects its role in aggregate development. In parallel with unitary development, colonies are often founded by a single queen, along with her mate or mates. The mates can be present as actual adults, as in the termites, or as sperm stored in the queen's spermatheca. Colonies with multiple queens at some stage are not unusual (Crozier & Pamilo 1996), but in most cases high relatedness is maintained by a single-queen bottleneck at some point in the life cycle (Maynard Smith 1989). In some groups, such as *Polistes* wasps, one queen quickly becomes dominant and lays most of the eggs (Pardi 1948; Reeve 1991). In others, such as ants in which colonies are founded by multiple queens, the queens can reproduce more or less equitably for a time, but after the first workers emerge they fight to the death (Bourke & Franks 1995; Bernasconi & Strassmann 1999). In still others, such as the epiponine wasps, colonies with multiple egg-laying queens are the normal state, yet new cohorts of queens are reared only in colonies that have reduced to the level of about one queen (West-Eberhard 1978; Queller *et al.* 1988). In each case, relatedness within the colony is maintained at reasonably high levels by some form of bottleneck (Maynard Smith 1989).

Although social insects resemble unitary development in that they often start from a single propagule, they resemble aggregative development in having genetic variation within the colony. The single queen and her mate produce an array of genotypes, and this lack of clonality opens the door to conflicts of interest. This probably accounts for a major difference between the basic structures created by standard single-cell development transition and the transition to social insect colonies. As an animal develops, many of its cells divide, including those in somatic lineages. In contrast, the social insect queen is the sole source of the analogues of both somatic and germ cells, that is, of both the sterile workers and the sexual reproductives. Imagine that it were otherwise, that the queen produced a first brood of daughters, who mated and produced the next brood, and so on. Soon relatedness would drop to very low levels and sociality could no longer be sustained. It is interesting that slime moulds, which might be like social insects in having genetic variation within their groups, follow a similar path to the social insects, in the sense that there is no cell division after the aggregate has formed.

(d) *Origins of sociality and relatedness*

Curiously, as long as only the queen reproduces, the presence of genetic variation in social insect colonies does not necessarily cause the initial conditions for cooperation to be any less favourable than they are in clonal development. If a single queen has mated once, her offspring will be full siblings, related to each other by 1/2 (for haplodiploid females, this is the average of relatedness to an equal number of brothers and sisters). Their relatedness to their own offspring is also 1/2, so the question of whether they should rear siblings instead of offspring boils down to whether $b > c$, as before. In spite of this parallel, and in spite of the fact that conditions leading to $b > c$ can readily be identified (Reeve 1991; Queller & Strassmann 1998), considerable effort has been put into making relatedness the prime mover in the evolution of sociality, that is, finding conditions in which relatedness to siblings is higher than relatedness to offspring ($r_b > r_c$) (Trivers & Hare 1976; Seger 1983; Grafen 1986; Godfray & Grafen 1988).

These efforts began with the initial exposition by Hamilton (1964*a,b*) of the idea of kin selection (Maynard Smith 1964), and came to be closely identified with it. Besides deriving the general theory of kin selection, Hamilton noticed a very curious juxtaposition of facts: (i) most social insects are haplodiploid ants, bees and wasps; (ii) haplodiploid full sisters are related by 3/4 because their father contributes his entire haploid genotype to each daughter; and (iii) workers in the haplodiploid species are invariably female. Perhaps this unusually high relatedness is the reason that sociality is so common in haplodiploids. Females can gain more by rearing sisters than by rearing their own offspring.

Unfortunately for a beautiful idea, problems emerge when brothers are taken into account. Although female workers gain extra relatedness to their sisters, they get correspondingly less, 1/4, to their brothers. If they rear an equal mixture of the two, the average relatedness to the brood reared remains 1/2. With female-biased sex ratios, helping can sometimes be favoured, and selection on workers will drive the sex ratios to be female biased (Trivers & Hare 1976). However, the advantage is generally transitory. Once a social population has reached the optimal worker ratio—three females to one male when there is one singly mated queen—the relatedness advantage of rearing workers is exactly counterbalanced by the lower reproductive value of females (Grafen 1986; Crozier & Pamilo 1996). If there are also some females in the population who are non-social (producing no workers), then the relatedness advantage to helping in the social colonies can be sustained because workers can then avoid male production altogether. This can occur, for example, through overlapping social and non-social

generations (Seger 1983), or through some females' being unmated and therefore unable to rear either workers or female reproductives (Godfray & Grafen 1988). Again, these advantages are transitory in that they do not persist once the species is entirely social.

Another model that would give workers an advantage unfolds if workers lay male eggs, something they can do without mating (Trivers & Hare 1976). Then they could have the best of both worlds, rearing sisters instead of daughters (r = compared with 1/2) and sons instead of brothers (r = 1/2 compared with 1/4). Of course, if there were multiple workers in a colony, they would mainly be rearing each others' sons (r = 3/8 if the queen is singly mated), but that is still better than rearing their mother's sons.

It is difficult to assess empirically the importance of these relatedness-based explanations of the origin of sociality. Although workers in current social Hymenoptera sometimes produce males, more often they do not (Bourke 1988; Choe 1988), and this includes some primitively social species (see, for example, Arévalo *et al.* 1998). Workers frequently do seem to control sex investment ratios (Trivers & Hare 1976; Nonacs 1986; Queller & Strassmann 1998), but it remains uncertain whether the associated transitory advantage to sociality mattered in the origin of sociality. The benefit:cost ratio might have mattered more and worker sex ratio control might have evolved only after high benefit:cost ratios had established sociality.

The transition to multicellularity teaches us that no such relatedness-based mechanism is required to evolve cooperation. There, the relatedness gained from rearing a clone-mate's offspring is no higher than that from rearing one's own offspring, so that the evolution of multi-cellularity requires that $b > c$. As noted above, this is the same condition required for workers to raise full siblings instead of their own offspring, even without any special appeals to sex ratio or the laying of male eggs by workers. There are several strong candidates for factors that make $b > c$ in the early social insects (Queller & Strassmann 1988). However, even if Hamilton's specific haplodiploid hypothesis is not correct, his general theory is unaffected.

3. CONTROL OF CONFLICTS

If independent units are to come together into successful new organismal entities, there must be some means of controlling the conflicts between them, some means of ensuring that the old units do not continue to pursue their individual reproduction at the expense of the group (Maynard Smith & Szathmáry 1995). Such controls could have evolved for that purpose, or they could be secondary, having originally evolved for other reasons. For both the transition to multicellularity and the transition to colonies, the initial restraint on conflict comes from relatedness, and relatedness defines the range of potential conflicts that need to be controlled by other means.

(a) *Bottlenecks in unitary development*
Buss (1987) argued that conflicts might be a disruptive force in multicellular individuals. Cells could evolve selfish strategies that gain them a disproportionate share

of the individual's reproduction. They might, for example, replicate faster or eschew somatic tasks in favour of increasing their representation in germ cells. The evolution of individuality would require mechanisms of controlling such conflicts. However, Buss neglected the most important control: development from a single cell (Slatkin 1985; Seger 1988; Bell 1989; Maynard Smith 1989). Under unitary development, conflicts are minimal because the multicellular individual is a clone of cells. Conflicts can emerge only from new selfish mutations. Each such mutation benefits from only one episode of selfish behaviour, because in the next generation it will find itself in individuals having all selfish cells, i.e. with no non-selfish ones to exploit (Slatkin 1985; Seger 1988; Bell 1989; Maynard Smith 1989). Therefore, to be an important force, such mutations need to recur repeatedly, with the evolutionary force consisting of mutation pressure, augmented by only a single generation of within-individual selection for each mutation.

A few models have explored the evolution of selfish mutants that replicate at a higher rate than usual but at some cost to the whole organism (Michod 1996, 1997; Michod & Roze 1997). The models show that recurrent selfish mutants can be favoured under certain circumstances, indicating that selfish behaviour can be a threat even to clonal organisms in which each mutation gains only one generation of within-individual advantage. However, rather special conditions are required. First, the mutation rate to the selfish form must be fairly high, generally 10^{-5} or higher. Michod (1997) argues that such rates are plausible for two reasons. First, mutation rates might have been much higher before the transition to multicellularity than they are now. However, modern unicellular and multicellular organisms seem to have about the same mutation rates per base pair per replication (Drake *et al.* 1998), so it seems unlikely that the unicellular ancestors of multicellular lines were much different. Second, the assumed high mutation rate at single loci might give a reasonable approximation to the sum of lower rates at many loci affecting the cell division rate. This seems reasonable, although the number of loci involved is unknown.

A second requirement for successful selection for selfishness in these models is a rather large number of cell divisions. More cell divisions means more occasions for the relevant mutations to occur, and more division cycles in which such mutants can express their replication advantage during the one organismal generation to which it applies. Little within-organism change occurs in the models with fewer than 20 or 30 cell generations, corresponding to about 10^6 and 10^9 cells, respectively. For comparison, the adult of the nematode *Caenorhabditis elegans* has fewer than 10^3 cells (Sulston & Horvitz 1977). This is of course small for a metazoan, but it seems reasonable to presume that the first metazoans were small. Controls other than the single-cell bottleneck were therefore probably not very important in the earliest evolution of multicellular forms but could come into play with larger organisms.

(b) *Relatedness conflicts in social insects*
In social insects, relatedness alone offers much less secure control over conflicts than it does in multicellular

clonal groups of cells. As noted in §2(c), this might explain the striking fact that, whereas many cells divide in multicellular individuals, reproduction in social insects is limited to the queen (and her mates). Even with only the queen reproducing, colonies are not generally clones. Selfish alleles are therefore not limited to one generation of within-colony selection. There will always be potential conflicts between genetically different individuals within colonies. However, potential conflict might sometimes be controlled so that actual conflict is minimized (Ratnieks & Reeve 1992), and control of actual conflicts is what is important for the consolidation of a new organismal level.

Two branches of the apid bees, honeybees (genus *Apis*) and stingless bees (tribe Meliponini), will be used to illustrate the major kinds of conflict that remain, even in highly eusocial insects with morphologically differentiated castes. They will also serve to demonstrate the difference between potential and actual conflict. The two taxa have similar colony cycles, with colonies being headed by a single queen, and new colonies being formed by swarms of workers accompanying a queen. However, the genetic structures of their colonies differ, because stingless-bee queens are generally singly mated (Contel & Kerr 1976; Peters *et al.* 1999), whereas honeybee queens mate numerous times (Estoup *et al.* 1994; Oldroyd *et al.* 1997). This has important consequences for several kinds of conflict (Peters *et al.* 1999) (see table 2).

Mate number affects the relatedness values determining whether workers should allow each other to lay the male eggs (Starr 1984; Woyciechowski & Lomnicki 1987; Ratnieks 1988). For the honeybees, in which the queen has mated multiple times, the worker choice is between their mother's sons ($r = 1/4$) and their half-sisters' sons ($r = 1/8$). Consequently, they choose the former, and the queen lays nearly all of the male-destined eggs (Ratnieks & Visscher 1989). Workers rarely attempt to lay eggs; when they do, the eggs are eaten by other workers. In effect, each worker agrees with the queen that other workers should not be allowed to reproduce. The workers' choice in the singly mated stingless bees is different. They can raise their mother's sons ($r = 1/4$) or their full sisters' sons ($r = 3/8$). Workers should therefore not police each other (Ratnieks 1988), and conflict is expected as both the queen and the workers attempt to produce the males. This is what is observed: egg laying in stingless bees is surrounded by elaborate rituals suggesting conflict between the queen and workers (Crespi 1992; Zucchi 1993). If worker-laid eggs are eaten, it is generally by the queen rather than by other workers, and workers sometimes succeed in producing significant numbers of males (Contel & Kerr 1976; Beig 1972; Zucchi 1993).

A second kind of conflict involves daughter queens. Daughter queens are needed for the production of new colonies, and they can also be useful to have on hand to replace a mother queen that dies. However, daughter queens also represent a potential threat to the established queen (Peters *et al.* 1999). The daughter queen is more related to her own offspring than to those of the old queen, so she should prefer to replace the old queen's offspring with her own. There is a range of benefit:cost ratios within which she should risk trying to depose the old queen and use the colony's resources for herself (Peters *et al.* 1999). Under multiple mating, this range of

Table 2. *Social differences between honeybees and stingless bees*
(From Peters *et al.* (1999).)

trait	honeybees	stingless bees
worker oviposition	rare	common
who eats worker-laid eggs	other workers	usually queen
who produces males in queen-right colonies	queens	sometimes workers
ritualized conflict over oviposition	no	yes
reserve of adult daughter queens	no	yes
who leaves nest during swarming	mother queen	daughter queen

benefit:cost ratios is large, whereas under single mating the range is small. Therefore daughter queens are a greater potential threat in the multiply mated honeybees than in the singly mated stingless bees.

Honeybees avoid this threat in an unusual manner. The old queen never comes into contact with daughter queens because, when the time comes to swarm, the old queen leaves the colony before the daughter emerges. She can afford to do this because the workers' interests are aligned with hers on the issue of how the colony should be divided and she leaves with most of the workers, laden with food stores (Peters *et al.* 1999).

In stingless bees, where new daughter queens are less of a potential threat, adult daughter queens are often tolerated within the colony and are available to take over should the old queen fail. Most are never needed for this function, so there might end up being some actual conflict: the non-needed virgin queens are often executed by the workers (Imperatriz-Fonseca & Zucchi 1995).

Two additional factors that we did not incorporate before (Peters *et al.* 1999) also influence queen rearing: conflicts over the sex ratio and over caste determination. When the queen is mated many times, workers are equally related to sisters and brothers ($r = 1/4$) and are therefore selected to favour a 1:1 sex investment ratio, exactly the same as the queen, who is equally related to her sons and daughters. However, as noted above, when the queen is singly mated, as in stingless bees, workers are three times more related to their sisters ($r = 3/4$) than to their brothers ($r = 1/4$), so they are selected to invest three times as much in females (Trivers & Hare 1976). Much evidence in social insects suggests that workers usually control the sex investment ratio (Trivers & Hare 1976; Nonacs 1986; Queller & Strassmann 1998). In the stingless bees, one way in which workers can make the investment more female biased is to swarm more often than the queen would prefer, and this requires more frequent rearing of daughter queens. There is no such need in honeybees.

A final factor that might affect queen rearing is whether an individual female can control her own fate and become a queen, possibly against the interests of the old queen and workers (Bourke & Ratnieks 1999). Again, other things being equal, this conflict is expected to be

more intense in multiply mated honeybees. However, honeybees, as well as many stingless bees, rear their queens in special cells with special food. Conflict is avoided because the individual female has no real choice (Bourke & Ratnieks 1999). In contrast, stingless bees of the genus *Melipona* rear their queens in the same cells and with the same food as workers. A developing female might therefore choose to be a queen or a worker (Bourke & Ratnieks 1999), and this genus shows a spectacular overproduction of queens, most of which are later executed.

These examples show that potential conflicts can either result in actual conflict or be controlled. Thus, with respect to male production, honeybees have less potential conflict and less actual conflict than stingless bees. With respect to daughter queens, honeybees have greater potential conflict but have evolved an avoidance strategy that solves the problem. The stingless bees have lower potential conflict but have evolved no avoidance strategy, and are left with more actual conflict, particularly in *Melipona*.

(c) *Recognition*

There is another kind of relatedness-enhancing mechanism common to multicellular individuals and social insect colonies. Both generally have evolved recognition mechanisms. These ensure that the benefits of altruism flow to those who share the altruism genes. Failures of recognition can lead to colonies' being lost to usurping queens (Field 1992) or even to germ lines' being taken over by another individual (Stoner *et al*. 1999). However, there is a problem in the evolution of such systems, at least when they depend on sharing of variable genetic loci. Common alleles at such loci will generally be favoured because possessors of common alleles will find more cooperative partners and fewer aggressive antagonists (Crozier 1986; Grosberg 1988). Therefore, recognition systems might depend on variation maintained for other reasons (Crozier 1986).

Another kind of recognition could increase rather than decrease conflicts. If individual social insects could recognize their closest relatives within the colony, they would be expected to favour these relatives in many circumstances. For example, when a new honeybee queen is reared, each worker should favour rearing one who is her own full sister. However, current evidence suggests that social insects, including honeybees, do not generally discriminate in this way, or do so only very weakly (Breed *et al*. 1994; Keller 1977). It is not clear why this is so. Perhaps such recognition is too prone to costly errors, or perhaps recognition cues are masked or spread throughout the colony to reduce conflicts (Keller 1997).

(d) *Power asymmetries*

Conflicts are likely to be settled most easily if there is some power asymmetry between the conflicting parties. Two common and effective kinds of power asymmetry are timing asymmetries and numerical asymmetries. Timing asymmetries can work two ways. In the first, the party that is able to act first is able to constrain the strategy set of the other party. The clearest example is in caste determination, which usually depends on the quantity or quality of food provided (Wheeler 1991). An individual might prefer, other things being equal, to be a queen

rather than a worker, but if it is not provided with enough food, its best option might be to change to being a worker (Bourke & Ratnieks 1999). It has been argued that parental manipulation of food supply could have been important even in the early evolution of worker castes (Alexander 1974).

Buss (1987) has suggested that a similar kind of timing asymmetry might operate in early development. The earliest embryo stages are often controlled by the expression of maternal genes rather than offspring genes; this could serve to reduce conflicts between cell lineages in the early embryo. However, this is at best a very limited control mechanism because its action is restricted to the very early stages (Maynard Smith & Szathmáry 1995). Recall also that conflicts are least likely at the early stages, where there have been few cell divisions and little opportunity for the selfish mutations required for conflicts.

In contrast, if the first party's actions do not sufficiently constrain those of the second party, the opportunity to act last might be an advantage. This might explain why workers seem to control sex investment ratios. The queen controls the initial sex ratio, but because workers rear the brood they have final control over investment, and often act to reduce investment in males by selective cannibalism (Trivers & Hare 1976; Aron *et al*. 1995; Chapuisat *et al*. 1997).

Workers in social insects also have a numerical advantage in conflicts with the queen. Workers can be in many places at once, doing many things, whereas the queen cannot. As we have seen in the context of male production, the numerical advantage of workers as a whole can even be turned against individual workers who try to produce males (Starr 1984; Woyciechowski & Lomnicki 1987; Ratnieks 1988). Still, the simplest application of worker policing theory is not completely successful. Workers in multiply mated honeybees police effectively, as predicted, and workers in singly mated stingless bees apparently try to reproduce more. The problem is that, even in stingless bees, in which workers are predicted not to police each other, queens sometimes lay some or all of the male eggs (Machado *et al*. 1984; Zucchi 1993). The problem seems to be quite general. Most social insects seem to be singly mated (Boomsma & Ratnieks 1996), and most social insects do not seem to have male production by workers in the presence of the queen (Bourke 1988; Choe 1988). Clearly, relatedness is not all that matters, and reproduction by the queen might have other advantages to workers, perhaps having to do more directly with the efficient division of labour. The question is important because it is not limited to the production of males. We need to know why workers generally consent to the reproductive dominance of the queen.

Strength asymmetries between individuals might also settle conflicts, but probably less decisively and with more cost. This is because individuals are likely to be relatively equally matched when there are no asymmetries of timing or numbers. For example, foundresses in *Polistes* wasps can have more or less prolonged fighting over who gets to be the dominant egg layer (Reeve 1991).

(e) *The germ line*

Buss (1987) suggested that the early sequestration of the germ line evolved to control conflicts in multicellular

organisms. By keeping most cells out of the pool that will give rise to gametes, most potential conflicts can be averted. Models have confirmed that this measure can be effective (Michod 1996; Michod & Roze 1997).

However, a simple alternative explanation is that the germ line might have originated as a consequence of other cell lineages' altruistically removing themselves from the reproductive line, to perform some somatic benefit to the organism. Such altruistic forms can easily evolve. They should not be as vulnerable to within-individual selfishness as the cooperative mutants in Michod's models (Michod 1996, 1997; Michod & Roze 1997). The reason is that Michod's growth rate mutants are unconditional; the mutation is always expressed in every cell that possesses it. In contrast, a mutation that altruistically removes its lineage from the germ line must be expressed conditionally. It will code for instructions of the form 'if I am in position X at developmental stage Y, perform the altruistic developmental act'. When those conditions do not apply, it will take no action. Organized development works through conditionally expressed genes and, as noted earlier, such conditionality is important for altruism because it allows the benefits of altruism to go to cells that possess, but do not express, the same allele.

Recall that under unitary development, each mutation experiences only one generation of within-individual selection, and that the success of selfish variants depends on a large number of mutations' experiencing this temporary effect. When the altruism gene is expressed conditionally, even this one-generation effect is experienced only rarely. Consider an altruism allele that is expressed conditionally only when it finds itself in a particular time and place. To illustrate, let us say that this action cell is a specifiable one of the 16 cells present after four rounds of cell division. The altruism allele takes the action cell, and its descendant lineage, out of the reproductive line to perform some somatic benefit, whereas the selfish allele keeps these cells in the competition for the germ line. Mutations to this altruistic allele will experience the within-individual selective disadvantage only when the mutation events occur in the action cell itself, or in one of the three cells immediately ancestral to it. The zygote is not included in this group because any mutations that it possesses will be inherited by the whole organism. Mutations occurring in cell lines lateral to the action cell will result in chimaeras, yet there is no within-individual selection in their first generation because they have no opportunity to express themselves. In the next generation they will give rise to genetically uniform clones. The same is true for mutations in the descendants of the action cell. In general, if the action cell is in the *n*th round of cell division, there are only *n* cells that can mutate in a way that gives rise to within-individual competition, regardless of how many cell divisions occur in the whole developmental plan. Of course many conditional mutations will be expressed not just in a single cell but in a group of cells, but as long as this group is a small minority, the principle remains the same. Most mutations do not lead to any within-individual selection, so between-individual selection will be much more important.

Thus, the germ line arose as the cell lineages remaining after a number of sequential rounds of selection for conditionally expressed mutants that altruistically put themselves into the soma. There does not seem to be any need to invoke selective exclusion of some lines by others. However, even if the germ line evolved in this manner, it might still have been advantageous to add controls such as reduced numbers of cell divisions and reduced mutation rates (Michod 1996; Michod & Roze 1997).

4. WHAT IS THE ORGANISM?

Life on Earth has undergone a series of major transitions, many of which created new levels of organization: cells, eukaryotes, multicellular individuals and colonies (Maynard Smith & Szathmáry 1995). Except for the earliest stages, about which we can only make intelligent guesses, the old levels of organization remain along with the new. We still have prokaryotes; indeed they are a dominant form of life (Gould 1996). We still have unicellular eukaryotes, and we still have multicellular individuals that have not seen fit to organize themselves into organismal colonies. Clearly, the units that we consider to be individual organisms are not defined by their having achieved a certain rung on the ladder of life or by having acquired a certain level of organization. What, then, does define the organism?

The definition that seems most consistent with both past usage and present theoretical understanding is that the organism is a consolidated unit of design, a unit whose traits are all selected to work together in nearly perfect harmony for the survival and reproduction of the whole (Queller 1997). This is quite close in meaning to the definition in Webster's *New collegiate dictionary*: 'a complex structure of independent and subordinate elements whose relations and properties are largely determined by their function in the whole'. This definition implies both the presence of cooperation and the absence of significant actual conflicts, because conflicts mean that some of the properties are determined by something other than their function in the whole. The organism is the result of a powerful history of selection at that level, and weak or no selection within that level, a pattern of selection that results from advantages in cooperation and effective control of conflicts. In this view there is no contradiction in viewing a prokaryotic cell, a fruitfly, and a honeybee colony as organisms.

Viewing social insect colonies as organisms does deviate from common usage, but there is still considerable precedent. For example, Wheeler's paper 'The ant colony as organism' (Wheeler 1911) makes precisely this argument. If the colony is an adapted unit in the same way that conventional individuals are adapted, then why treat it differently? Wheeler and others later shifted to the term 'superorganism' to indicate that a colony was a sort of organism built from other organisms, but I think that the distinction is no longer needed given that conventional organisms have also been built from lower-level organisms. So, if it seems to be time for a revival of the view that social insect colonies can be superorganisms (Seeley 1989; Wilson & Sober 1989; Moritz & Southwick 1992), then I would suggest that it is more consistent to simply view them as organisms.

Several authors have recently attempted to make the case that the honeybee colony is a superorganism (Seeley

1989; Moritz & Southwick 1992). I agree with their conclusion, but I think that the argument needs to be strengthened. They focus primarily, although not exclusively, on evidence that colonies behave in ways that are adaptive for colony survival and reproduction. Foraging, construction, communication, brood care, and defence are coordinated in adaptive and often elaborate fashion (see also Winston 1987; Seeley 1996). This certainly establishes that there are strong strains of cooperation and integration, but this is the easy part of the case, and it can probably be established for any social insect. What needs to be shown in addition is that conflicts are minimal (Seeley 1989), near the low levels seen in other entities that we consider to be organisms (Hurst *et al.* 1996). I think that such a case can be made for honeybees. As noted above, multiple mating by the queen has affected all of the major kinds of within-colony conflict discussed. First, it has removed even potential conflict over the sex ratio. Second, it has created a situation in which workers, as a group, will thwart any worker who individually tries to lay male-destined eggs. This leads to effective self-policing by workers, so that there is little actual conflict over male production. Third, multiple mating increases potential conflict between the mother queen and her daughter queens, but all actual conflict is avoided by the departure of the mother queen before daughters emerge. Multiple mating also enhances the potential for conflict between patrilines but, as noted above, there seems to be little actual conflict of this type. One kind of clear conflict remains. When the old queen departs there are usually multiple daughter queens about to emerge. The first to emerge can choose to leave with a secondary swarm, or she can choose to stay, in which case she seeks out and kills her sister queens. Although this is undeniably conflict, it does not seem to me much more severe than the kinds of conflict that we see within conventional organisms (Hurst *et al.* 1996). Thus, honeybee colonies would seem to qualify as organisms on account of both their extensive integration and cooperation, and their near absence of actual costly conflicts.

I would not necessarily argue that all social insects have organismal colonies. All have fairly extensive cooperation, but some might fail the test of minimal conflicts. Stingless bees have more conflicts than honeybees, although some of these might be ritualized relics of past conflicts. *Polistes* wasps seem to expend much effort in overt dominance behaviours, with the most dominant female being the main reproducer (Reeve 1991). In the ant, *Formica execta*, considerable wasted effort seems to be expended in conflicts over sex investment (Chapuisat *et al.* 1997). Whether expensive conflict over a single issue is enough to disqualify such colonies from organismal status is not clear. It is probably foolish to assume that there will be a clear demarcation between organismal and non-organismal social insects, but that some have reached the organismal state is an important point.

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