Sex-ratio conflicts, kin selection, and the evolution of altruism

Wladimir J. Alonso* and Cynthia Schuck-Paim

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom

Edited by Edward O. Wilson, Harvard University, Cambridge, MA, and approved March 6, 2002 (received for review November 1, 2001)

Kin-selection theory has thrived in the explanation of a wide variety of biological phenomena, chiefly the evolution of biological altruism as that found in sterile castes of eusocial insects. Much of the way in which it has been tested is based on the existence of conflicts over sex-ratio production within eusocial colonies. However, despite neatly showing eusocial colonies as arenas where selection at the gene level triggers the appearance of sophisticated patterns of animal behavior, being often regarded as one of the most (or even the most) important evolutionary insights of the recently finished century (5). Among its greatest contributions is the formulation of an evolutionarily acceptable framework for the appearance and maintenance of the so-called biological “altruism,” through which individuals behave by lowering their own potential for reproduction or survival in favor of the reproduction of other individuals of the same species.

A central problem addressed under the theory’s scope is the evolution of sterile castes of workers in colonies of eusocial (6–8) organisms, such as ants, termites, and some bees and wasps. According to the theory, the evolution of worker castes was possible only because of the success of genes (hereafter “altruistic genes”) codifying for behaviors whereby their carriers sacrifice their own reproductive output by helping the reproduction of individuals who most likely have these genes. The conditions for these genes to spread are given in the well-known Hamilton rule (9): \( rb - c > 0 \), where \( r \) is the coefficient of kinship between the altruist and the receiver of the altruism, \( b \) is the benefit in terms of extra offspring for the receiver of the altruistic act and \( c \) is the cost for the altruist’s offspring production.

An alternative explanation for the emergence and evolution of sterile castes in eusocial organisms states that the characteristic (or “gene,” in the present operational language) under selection is one that imposes the nonreproductive role to part of the brood, by handicapping its full reproductive development through a shortage of resources and/or agonistic interactions (“parental-manipulation theory” (10, 11); see also refs. 12–17). As a result, the eusocial system would not emerge because of the expression of altruistic genes, but instead because of the evolutionary advantage provided by a developmental process comprising several individuals, functioning at a new level of selection (the eusocial colony).

Nowadays some kin-selection defenders support the idea that the two theories are complementary, and that in fact the role of manipulation is to create better conditions for the fixation of the altruistic gene (9, 18). Although the idea is consistent with the internal logic of kin-selection theory, it leaves unanswered the question of when, during the evolution or development of a eusocial colony, it would be unequivocally necessary to invoke the existence of a kin-selected altruistic gene. Crozier (18) proposes that a “nonresponse to manipulation” could be considered as an altruistic gene in the kin-selectionist sense. The argument, however, is not helpful for the identification and description of evolutionary innovations, as in that same line of reasoning (and so playing the game of working in an “all is adaptive” world) that lack of response could be also regarded as an adaptation of the new level of organization represented by the colony. It has been also postulated that what we sometimes see as manipulative devices in eusocial colonies (such as pheromonal control and aggressive interactions) would in fact be signals to allow those individuals possessing the altruistic gene to decide whether or not to help the signaling party (19–21). The fact that the manipulation could operate through signals more than through direct inhibitors is also accommodated by the logic of the manipulation theory: efficient communication systems are expected to evolve inside an organism (as a eusocial colony can be considered) once it has been already established, replacing the direct inhibition systems that once allowed its formation. In fact, indirect and ritualized forms of communication are observed predominantly in highly eusocial organisms, whereas in primitively eusocial societies, dominant individuals rely on more direct forms of aggression (7, 8, 13).

Although it is not our aim to defend one theory against the other, it is necessary to mention that the main argument broadly used to undermine manipulation theory (9, 22) in fact does not affect it. The argument is based on the analysis of the viability of a eusocial system evolving through the manipulative route when strategies of resistance to manipulation arise in the manipulated individuals. As any genetic system, a eusocial colony is certainly exposed to disruption of its organization due to the invasion of selfish strategies among the lower levels of organization, and as so only those systems able to cope with it through the fixation of compensatory or suppressor strategies (see below) will be able to survive. An invasion by selfish or opportunistic...
strategies is certainly also a “problem” that a colony evolving through kin selection would have to face. Kin selection “solves” this problem simply by imposing in its basic formulation (Hamilton’s rule, above) that the overall genetic benefit for the altruistic gene has to be positive so that the altruistic behavior can spread. If we follow the same line of reasoning, manipulative genes could also just demand a beneficial outcome for the spread of manipulative actions. The argument therefore does not provide useful insights as to which theory better explains the evolution of altruism in eusocial colonies. That is why it is important to clearly establish in which aspects the theories can be really distinguished and tested.

In fact, if kin-selection literature is carefully scrutinized, one can notice that several of the studies designed to test the role of kin selection on the evolution of eusociality are not comparisons of its predictions against those of other hypotheses, but solutions to the problems that the acceptance of kin selection itself poses. For instance, Queller (23) states that a prediction of kin selection is that “colony mates must be related and that sterility must be conditionally expressed.” Because those are well-established facts, this theory would be strongly supported. However, the conditionality of the worker–queen trait is not a prediction of kin selection, but simply an aspect of the generation of division of labor inside the colony that any theory should explain, and not restate as a prediction. In the same way, the search for higher degrees of relatedness is not a test against manipulation theory, for this theory too is based on a process that takes place within the same familiar brood (so that the developmental mechanism under selection can be passed on to the next generation). In fact, it is only a search for the conditions for the fixation of the altruistic gene, and as such, an internal problem for kin selection [that is, finding the conditions foreseen by this theory does not necessarily imply the existence of kin-selected altruistic genes, it only implies that the conditions exist for them to be fixed (12)].

Yet, quantitative tests of Hamilton’s rule have not proved an easy task (23–28). As pointed out by Bourke (24), attempts to accurately measure offspring numbers gained and lost through altruism have met many obstacles. Additionally, it has been shown that, owing to the occurrence of competition between relatives, estimates of even high degrees of relatedness are not sufficient evidence for the role of kin selection in promoting altruism (27, 28).

**Sex-Ratio Conflicts and Eusociality**

Given the difficulties previously mentioned, one of the predominant ways of testing the theory has been the investigation of its predictions regarding the existence of sex-ratio conflicts within societies (9, 20, 23–25, 27, 29–31). As Chapuisat and Keller (25) highlight, “empirical tests of kin selection have proved difficult, because social behavior has been shaped by the interaction of multiple ecological and genetic factors over evolutionary time. Studies of sex allocation in hymenopteran societies have emerged as prime tests of kin selection because sex-allocation theory provides quantitative predictions based on variation in relatedness.” Indeed, the outcome of such tests has been seen as extremely favorable, as Queller and Strassmann (31) point out: “the most striking support for kin-selection theory from any organism comes from studies of sex ratios.”

However, here we argue that because altruism is not involved in these conflicts, the approach gives only limited support for the role of kin-selected genes on the evolution of eusociality. We also remark the existence of alternative theories for the phenomena, and finally we highlight that explanations based on the occurrence of sex-ratio conflicts have been frequently overused when simpler explanations based on an organism’s life history or phylogenetic constraints are also available.

Kin-selection predictions’ on sex-ratio conflicts were developed from the application of the sex-ratio theory of Fisher (32) to kin selection by Trivers and Hare (33). As mentioned, altruistic genes should make their bearers benefit preferentially the class of individuals who most likely share the same genes to promote their spread. In monogynous hymenopteran societies headed by a single-mated queen, workers are highly related to their sisters, and would pass on their genes three times more efficiently through sisters than through brothers. The queen, on the other hand, has the same degree of relatedness with both sons and daughters. Following this logic, Trivers and Hare (33) proposed that conflicts of interests over sex ratios should exist between the queen and her worker progeny, because while workers would be interested preferentially in the production of females, the queen should be interested in the maintenance of a Fisherian 1:1 ratio among its reproductive brood. Support for the theory would therefore come if individuals behaved by biasing the sex ratio in accordance to their genetic interests. From the same perspective, a diverse set of predictions can be derived if the genetic structure of the colony and population increases in complexity, which may happen because of the presence of several queens in a colony, multiple mating, and/or reproduction of the workers (9, 20, 23–25, 29–31).

Within this theoretical framework, a number of studies have shown eusocial colonies as arenas where the selection at the gene level triggers the appearance of sophisticated disputes aimed at one’s own genetic overrepresentation. Nevertheless, a closer analysis reveals the limitations of the potential of such genes in the evolution of eusociality. To illustrate this, we examine some representative examples selected from the vast literature on the subject. To avoid personal bias, we use the same selection as that used in a recent paper (24) aimed at explaining the success of kin-selection theory based on studies of social conflicts in eusocial insects.

Sundstrom et al. (34) found that workers of the wood ant *Formica exsecta* were killing the male larvae in single-mated queen colonies, but not in multiple-mated queen colonies. The behavior can be thus interpreted in accordance with the Trivers and Hare (33) model, because in the former case workers would prefer to raise sexual females, to whom they share a higher degree of relatedness, instead of males. In the latter case, however, the interest of workers over the sex ratio would coincide with that of the queen—and so they should rear all brood produced.

Another example that is presented as “explained by kin selection and by no other theory” (24) is the case of worker policing (35–38). It states that workers in haplodiploid colonies should be selected to allow—or instead “police”—the process of egg laying by other workers depending on the degree of relatedness among the workers, and among the workers and the queen(s). In single-queen, single-mated colonies workers would be more related to each other’s sons than to the queen’s sons, and therefore allowed to lay the unfertilized, male-producing eggs. In polygynous or multiple-mated queen colonies, however, workers would benefit by suppressing each other’s egg laying in favor of the queen’s male offspring. Within this perspective, Foster and Ratnieks (39) studied the social wasp *Dolichovespula saxonica*, a model species for testing the worker-policing hypothesis as the mating frequency of single queens present in each colony varies among colonies. They indeed confirmed the outlined prediction: in single-mated queen colonies the proportion (70%) of male eggs reaching adulthood did not differ between those produced by workers and by the queen. On the other hand, in multiple-mated queen colonies only 10% of the male eggs laid by workers reached adulthood (as opposed to 75% laid by the queen).

However, a closer analysis of these examples and others involving sex-ratio conflicts shows us a common denominator in the behavior of workers: the individuals performing these acts are not paying any cost in terms of Darwinian fitness by behaving in those ways. We could describe the action of the genes involved...
as codifying the following instructions in workers: in the first example “kill brothers when you are daughter of a single-mated mother,” and in the second example “kill workers’ eggs when you are daughter of a single-mated mother.” Yet, although the codified behaviors indeed favor the spread of copies of the genes promoting them, they do not bear any direct fitness cost to performers or can be thought of as the ones that could have led them into a sterile condition. As previously exposed, kin selection was presented as a novelty because it would explain the evolution of altruistic behaviors, and among all of the definitions for biological altruism, at least it is agreed that the individual has to suffer a loss in either its direct reproduction or survival when performing the altruistic act. To test the theory as an explanation for eusocial evolution it is thus not sufficient to show that there are genes or strategies that at no cost, and making profit of an already established social organization, can promote their own spread by distorting sex ratios.

Additionally, once it is considered that the behaviors performed by workers in sex-ratio conflicts bear no cost in the sense previously defined, the use of Hamilton’s rule is not essential to understand the phenomena. For example, when the eusocial colony is functionally and evolutionarily regarded as an organism or “superorganism” and thus as a unit of selection (9, 23, 40–42), and it is acknowledged that selection can take place at many interacting levels (with some genes, as another unit of selection, behaving selfishly to promote their overrepresentation), it seems simpler to understand the phenomena by considering the sex-ratio-distorter strategies found in eusocial colonies as analogs to the strategies used by some genes in conflicts emerging inside the genome of individual organisms. These “selfish genetic elements” (SGEs), as they are defined, have been demonstrated to act in organisms in several, and even dramatic, ways (43–46). They are vertically transmitted as genetic entities that manipulate their “host” to promote their own spread, usually at a cost to other genes within the genome. In the case of social insects, SGE frequency could be increased as a result of a differential expression according, for example, to the caste of the individual host. While in queens these units can spread directly through reproduction, for example, in workers a transmission advantage could be achieved through the expression of traits causing the death of (or spiteful behavior toward) individuals lacking copies of them.

The presence of SGEs also sets the context for the emergence of conflicts, as they make possible the spread of other genes (referred to as “suppressors,” see ref. 43) with opposite effects in the same organism. Because of their higher genetic diversity, colonies with several and/or multiple-mated queens are particularly exposed to invasion by some patri- or matriline-transmitted SGEs that can cause those workers inheriting them to behave “parasitically” by laying eggs and helping less in colony tasks (this has been found, for instance, in some strains of honey bees; refs. 47 and 48). Therefore, the fixation of suppressor strategies (worker policing in this case) could be explained simply as a mechanism of conflict control by the colony to avoid that kind of parasitism. In fact, a “colony-level benefit” argument is the one that many authors use in those cases where the existence (or absence) of worker policing contradicts kin selection predictions (49–51). Foster and Ratnieks (52) themselves apply it for Vespa vulgaris, when finding worker policing but failing to find evidence that workers were more related to the queen than to each other, or when finding worker policing in colonies with low effective paternity, in which workers of Vespa crabro were killing their closer relatives to favor more distant ones (53, 54). In these cases, they consider that the worker policing behavior “may be selected due to the colony-level benefit of conflict suppression.” As we have just described, the rationale applies not only to V. vulgaris and V. crabro, but to D. saxonica as well.

Needless to say, we do not claim that all conflicts over sex ratios should be interpreted under the SGE framework. However, it is our aim to highlight that plausible alternative explanations exist (see also ref. 17 for a review of alternative models of sex allocation in primitively social bees) to phenomena traditionally viewed under the exclusive approach of kin selection.

Sex-Ratio Conflicts and Social Biology of Organisms

It has been increasingly common to attempt explaining several aspects of the social biology of eusocial colonies as shaped by conflicts over sex ratios. Contrary to this approach, we argue that the analysis of social traits as by-products of sex-ratio conflicts has been frequently overused when simpler explanations based on an organism’s life history or phylogenetic constraints are also available. As a representative example we analyze the work of Peters et al. (55) on stingless bees (Meliponini), in which the authors confirm previous suggestions that single-mating is widespread in this group, as opposed to the multiple-mating system of honeybee queens. Because of the sex-ratio conflicts predicted for single-mating systems, stingless-bee workers should be in direct competition with the queen. From this principle, the authors take a further step in deducing the explanation of a series of biological traits particular to the group.

For instance, they advocate that the ritualized agonistic behaviors observed during the cell provisioning and oviposition process actually reflect the predicted existence of conflicts between workers and queens. However, a closer look at the biology of this group reveals fundamental differences in the way provisioning is performed (7, 56–58) as compared with that seen in honeybees. Stingless bees mass provision the brood cells before oviposition. The process can be highly variable between species but, as opposed to the process in honeybees, it usually demands a quick and continuous communication between the queen and workers so that all of its steps (e.g., signaling, provisioning, and sealing of the cell) can be properly accomplished. A highly efficient and intense communication system is thus required, and it seems difficult to imagine another way it could operate other than through direct interactions between the parties, benefiting from a preexistent behavioral repertoire.

In the same way, the fact that workers and males are reared in identical cells (contrary to Apis) is explained as a mechanism that evolved in this group to avoid conflicts “because male eggs laid in identifiable cells would be more easily removed by the opposing party.” However, the argument misses the very point that the evolutionary innovation of having different cell types for rearing males and females belongs to Apis, and Meliponinae only retains an ancestral feature, in which the mother (and in some cases the reproductive workers) decides the ploidy of the egg, regardless of the cell type. Additionally, the explanation does not address the really interesting innovation inside one of the stingless-bee groups, that is the fact that in the Meliponina genus all cells (not only for males and females, but also for queens and workers) are identical. If cells were identical to avoid the removal of male larva, why then would the cell of a queen be also identical, if workers are not interested (as they argue) in eliminating the excess of queens?

The tolerance of workers toward virgin queens in the stingless-bee nest is also explained from kin selection’s standpoint, because of their high degree of relatedness. It also seems simpler to acknowledge the fact that, given the complete sealing of the cell after the egg is laid, it is not possible to rear gynes in queenless colonies, and so there is always the need to maintain a stock of virgin queens to ensure the perenniality of the colony (7, 56, 59). Peters et al. (55) are contrary to this alternative explanation for believing that the sealing of the cell would not in reality be a constraint, as “in some species microqueens can emerge from worker cells, while in others, a worker larva can
become a queen by chewing into another cell to gain extra food.” However, the argument is not valid, because, apart from being restricted to a small group of species with different evolutionary histories within the stingless-bees’ group, it also fails to appreciate the fact that the production of microqueens or queens from worker cells is not triggered for the replacement of a queen exactly when it dies (we see no means how it could be), and thus cannot be a mechanism to ensure the perenniality of the colony without the constant maintenance of a virgin queen stock.

Conclusion

Hamilton’s rule provided a general framework for the understanding of the evolution of altruism by determining the conditions whereby actions causing an individual to behave to its own detriment would spread to fixation. Resulting from this would be the onset of eusociality, and in the same way the evolution of some other major biological transitions, chiefly the division of labor in multicellular organisms. Empirical tests of the rule have nonetheless proven difficult, owing to the multiplicity of ecological and genetic factors interacting in the evolution of social behavior, leaving for studies of sex-ratio conflicts the role of prime tests of the theory (23–25, 27). Keller and Reeve (20), summarizing a current consensus, conclude: “It is somewhat paradoxical that the outcome of within-colony conflicts provides one of the best demonstrations of kin-selection theory, a theory that was first proposed to explain the evolution of extreme altruism by determining the conditions without the constant maintenance of a virgin queen stock.

Without the constant maintenance of a virgin queen stock. Resulting from this would be the onset of eusociality, and in the same way the evolution of some other major biological transitions, chiefly the division of labor in multicellular organisms. Empirical tests of the rule have nonetheless proven difficult, owing to the multiplicity of ecological and genetic factors interacting in the evolution of social behavior, leaving for studies of sex-ratio conflicts the role of prime tests of the theory (23–25, 27). Keller and Reeve (20), summarizing a current consensus, conclude: “It is somewhat paradoxical that the outcome of within-colony conflicts provides one of the best demonstrations of kin-selection theory, a theory that was first proposed to explain the evolution of extreme altruism by determining the conditions without the constant maintenance of a virgin queen stock.

We are grateful to John Tyler Bonner, Gabriel Dover, Alex Kacelnik, and the anonymous referees for helpful comments on the manuscript. Financial support was received from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil (CAPES).