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THE ROLE OF KIN SELECTION THEORY ON THE EXPLANATION OF BIOLOGICAL ALTRUISM: A CRITICAL REVIEW

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Abstract. *Alonso, W.J. 1998. The role of Kin Selection Theory on the explanation of biological altruism: a critical review. J.Comp.Biol. 3(1):1-14.* The evolution of a large part of the sophisticated patterns of animal behaviour, such as altruism and eusociality, has been explained by the Kin Selection Theory. Because of its scope and implicit logic, this theory may not only be considered as a key point of sociobiology, but also as a paradigm of current evolutionary theory. However, there are many relevant problems related to it. Behaviours that are discussed into the scope of Kin Selection may favour directly the survival and reproduction of the performers. In other cases, these behaviours are by-products of developmental systems comprising many "individuals", each one performing a different task. Finally, where Kin Selection really models the spread and maintenance of altruistic acts, it overlaps the group selection theory.
Key Words. Eusociality, Altruism, Kin Selection, Parental Manipulation, Group Selection, Epigenetic Theory.

Introduction

The evolution of a large part of the sophisticated patterns of animal behavior, such as altruism[1] and eusociality, may be explained today by the Kin Selection Theory (henceforth, KS). Although it had been hinted at by some pioneer neo-Darwinian geneticists (Fisher, 1930; Haldane, 1955), it was widely formulated and developed by Hamilton (1963,1964,1972). Since then, a huge amount of studies have used it as a test model, and most results have been favourable to it.

Its scope includes an explanation for the evolution of sterile castes in eusocial colonies (a problem dating back to Darwin, 1859), the appearance of pluricellularity, the coloniality found in various marine invertebrates, the formation of family associations and groups in birds and mammals, and it was even linked, in a more polemic way, to the formation of certain human social patterns (Wilson, 1975). Therefore, due to its scope and implicit logic, it can be considered not only as a key point of sociobiology, but also as a paradigm of the evolutionary theory.

The present study intends to highlight some relevant problems related to KS logic and testability and to emphasize the existence of alternative and more parsimonious explanations for the problems commonly dealt with in the scope of KS theory. Before going further, a brief review of the basic the KS model is required.

Kin Selection

Usually, genes[2] remain in the genome of individual lineages if they either do not lower the fitness of their bearers (Gould, 1984), or provide greater success to the organism's machinery in its task of continuing to function and to reproduce. If by common ancestry the genes are not found exclusively in the body itself, but also in the bodies of kin, it may be more productive from the point of view of the cost/benefit ratio to help these kin to have additional offspring, rather than producing their own offspring. Therefore, the basic idea of the KS is that of *inclusive fitness*, a concept that breaks through the limitation imposed by the so-called Darwinian fitness, in which for a characteristic to have adaptive value it must favour its bearer's ability to reproduce.

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[1] Altruism is hereby defined according to Bertram (1982): "*Altruism, in biology, is defined as the behavior that probably increases the reproductive rates of individuals of the same species non descendants of the actor and, at least, at short term probably decreases the number of descendants of the actor itself*".

[2] Genes are not employed here as discrete portions of DNA , but using the definition of Williams (1966) as "*any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change*". Even so, when we state that something "is genetic" we simply mean that "*differences among phenotypes are causally associated with genotypic differences*" (Williams BJ, 1981).

Thus, inclusive fitness includes not only the fitness obtained by the individual through the transmission of its genes through reproduction itself (Darwinian fitness), but also the fitness obtained by the reproduction of its kin. A social act, according to the KS theory, is favored by natural selection if it results in an increase in the inclusive fitness of the individual.

However, certain conditions are necessary to be more advantageous for the individual to spend energy with kin that, otherwise, could be dedicated to its own reproduction. In this sense, the greater the degree of genetic similarity between two individuals, the greater the probability that an allele may be shared by two individuals. In the same way, the greater the increase in fitness for the benefited per unit of cost for the performer of the altruistic act, the greater the possibility that the gene codifying for this altruistic act will be fixed after its appearance. Therefore, for a gene that codifies such an act to become fixed in the population, the imposed condition is:

$$B/C > 1/r,$$

where

r = the coefficient of kinship between the altruist and the receiver of the altruism;
C = the cost in Darwinian fitness for the altruist;
B = the benefit in Darwinian fitness for the receiver of the altruistic act.

In the case of sexual diploid organisms, half of the genetic traits of the offspring comes from the random meiotic shuffle of the genome of each parent before fertilization. For this reason, each allele possesses an average probability of being found simultaneously in two siblings, which coincides with the probability of being found simultaneously between a parent and each one of its offspring. For this reason, from the point of view of inclusive fitness, it makes no difference if an offspring or a sibling are made viable (except for the greater certainty of parenthood over brotherhood). This "symmetry" does not occur in haplodiploid animals such as Hymenoptera (bees, ants, wasps), in which females usually develop from fertilized eggs and are diploid, whereas males develop from unfertilized eggs. In this sense each allele has a greater possibility of being found between sisters (r = , since they are identical on the father's side), rather than between a female and its offspring (r = °). In this way, these females would improve more in reproducing their genes through the investment in the creation of sisters rather than offspring and, then, the fact of eusociality having arisen so many times in this order of insects would be explained (details and recent reviews of this theory can be found in Hölldobler & Wilson, 1990; Bourke & Franks, 1995; Crozier & Pamilo, 1996; Choe & Crespi, 1997).

Direct benefits to individual survival

First of all, we have to consider that some phenomena that have been regarded as "altruistic" acts (and have therefore been discussed mainly in the KS scope) have also been reinterpreted as being directly beneficial to the survival and reproduction of their performers and, therefore, cannot be considered as altruistic. For example, in the case of the "warning calls" that apparently would benefit the group, exposing the sentinel to predation, Charnov & Krebs (1975) suggested that this act may in fact favor the "caller," who would benefit from the confusion caused, thus increasing its chance of flight[3]. Trivers (1971) attributed an advantage to the "caller" because, by preventing the successful hunting of the predator, the former would lower the frequency of the predator returning. Williams (1966) considered the alarm call made outside the breeding season as a simple by-product of this warning call made in order to alert mates and progeny (see also below for "non-adaptive altruism").

Aposematic coloring was also interpreted (ever since the pioneering vision of Ronald A. Fisher, 1930) as a mystery that can only be understood if we consider that the genes which confer a warning coloration may only be spread in an "altruistic" manner, since the predator that consumes an unpalatable prey item with a warning color would not consume another one if it had the gene conferring the same color. However, in studies such as those by Boyden (1976) and Wiklund & Järvi (1982) it was shown that there may be a direct increase in the survival probability of unpalatable and aposematic individuals themselves. Even considering the whole complexity of the question (*e.g.*, Guilford & MS Dawkins, 1993), one may not regard available data on this phenomenon as evidence of the KS.

Parental Care

Maternal care seems to be a widespread feature even among the insect taxa (*e.g.,* Tallamy &

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[3] The damage-released alarm was also shown to be beneficial to the prey caught by the fish *Pimephales promelas,* since the warning attracts other predators, thus possibly disrupting the predatory event (Chivers *et al.*, 1996).

Schaefer, 1997). Parental investment was defined by Trivers (1972) as "*any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring*" and "*will increase during evolution whenever a parent thereby improves its overall reproduction*" (Alexander, 1974). Therefore, if the progenitors are benefited, then, as pointed out by Darwin (1859), caring for one's progeny is an act that can be perfectly assimilated by the theory of natural selection acting on individuals that try to maximize their reproductive success. Nevertheless, some biologists (*e.g.*, Dawkins, 1979) understand that parental care is simply a category of KS. We could admit that (into the scope of the KS logic), but it is still not possible to consider parental care as a proof of KS theory, since the performer of this kind of behavior increases its own Darwinian fitness (increasing the descendant's chances of survival and reproduction) (Bertram, 1982; Brown, 1987; Blumstein *et al.*, 1997).

When analyzed carefully, some field data show that behaviors identified in principle as altruistic are, nevertheless, related to parental behavior. Again, the warning call supplies examples of this, as in the case of ground squirrels (Shields, 1980) and *Marmota flaviventris* (Blumstein *et al.*, 1997).

Non-adaptive altruism

It is also possible to think about the appearance and maintenance of some traits (and behaviors) without linking them with any adaptive value (Gould & Lewontin, 1979). For example, we can observe a kind of parental behavior directed toward individuals other than offspring if this phenomenon does not translate into a big cost to these "artificial parents", or if these costs are smaller than those linked to the creation of mechanisms against this "error". Actually, this might be the case of many birds that remain in their parental nest contributing to the care of siblings (the "*helpers*"). As proposed by many authors (ever since Williams, 1966, revised by Ligon, 1993), this may simply be an automatic and precocious expression of a trait that has an adaptive value only in the adult stage. The adoptions observed in some species might be so rare that they would have no importance from the evolutionary point of view[4] (Bertram, 1982; see also Huntingford, 1984).

The Group Selection Overlap

One obstacle for the fixation of an altruistic trait stems from the fact that its expression, besides directly diminishing the fitness of its bearer, would also not bring reproductive benefits to other bearers since, in the condition of "altruists" these other bearers are not able to have more offspring (every carrier of the altruistic trait could be merely a "compulsive altruist"). In face of that, we may imagine that in half of the interactions the altruistic gene acts as "*conventional*"[5], and in the other half it acts as "*altruist*" (*e.g.,* Maynard-Smith, 1982), or that the gene codifies the "*facultative altruism*" (Bourke & Franks, 1995). Nevertheless, without any more assumptions, during the times in that the *altruist* individual acts as *conventional*, it would be benefiting from this condition but, when it acts as *altruist*, it would be losing reproduction or survival in relation to those around it, which can be *conventional* or *altruistic* individuals. Therefore, the individuals possessing the *conventional* genes can receive fitness from the *altruists*, but the *altruists* will never receive fitness from the *conventional*. This means that the *conventional* genes, even in fairly unfavorable conditions, will take over the population (BJ Williams, 1981; DS Wilson, 1989).

The main consequence of this reasoning is that the benefits of altruism are not preferentially distributed among *altruists* than among *conventional* types if some "*special conditions*" are not fulfilled; and theories about the evolution of altruism look forward to these conditions. KS is based on the assumption that the population is structured in some degree (Michod, 1982) due to the limitation of dispersion of the individuals, or due to family behaviors, thus allowing for a great number of interactions among relatives (these are the *special conditions* of this model). These preferential interactions could help the spreading of altruistic behaviors since the "costs" of the behavior to the performer can be translated into "benefits" to some kin in the way foreseen by the formula previously presented.

But even if the interactions occur in structured families, this does not ensure that among kin, those that bear *altruistic* genes will receive a larger net benefit than the ones bearing *conventional*

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[4] Of course, as pointed out by West-Eberhard (1987), these adoptions may confer the previous conditions to possible social interactions (these ones with adaptive value).

[5] Here defined as the state which maximizes the reproduction of the individual that carries it. I avoid the term selfish, that is quite inflated with different meanings in sociobiology.
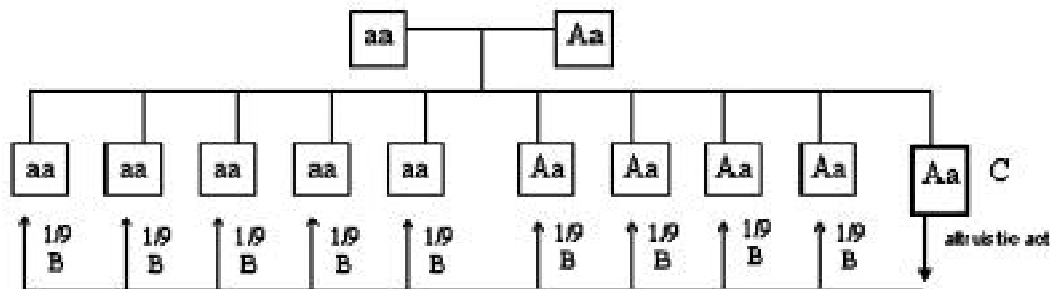
Figure 1. An example of thhe effect of a gene "A", being altruistic and dominant, aaand of a gene "a", selfish and recessive, in the offspring. In each altruistic act, all siblings receive an average benefit (B), but the cost (C) is only the individual who perform the act (DS Wilson, 1989).

genes[6] (Fig. 1) (DS Wilson, 1989).

The statement just presented may seem obvious, but it is really little understood, as shown by the fact that many studies simply present genetic similarity among relatives as a test of KS. It was also demonstrated that the limited dispersion of the individuals are not enough to spread the altruistic genes, because patches of altruists "*are unable to export their productivity to other regions of the landscape and are easily invaded by selfish types from neighbouring patches*" (DS Wilson *et al.*, 1992 and references therein). The possibility of escaping from this picture would only occur in two situations:

(1) If the altruist could recognize homozygotes and heterozygotes of the altruistic gene and preferentially direct the altruistic acts toward the homozygotes, which is rather difficult to conceive and currently has no empirical support (this recognition is not limited to simple degrees of kinship, as postulated in the "green beard effect" by Dawkins, 1976)[7].

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[6] It was hypothesized that heterozygous egotists would have larger benefits than the homozygous egotists. But which would be the mechanisms to attain it? Empirical evidences were not described.

[7] Many experiments were conducted to discover if there are mechanisms of kin recognition, and efforts in this area have resulted in the publication of whole books on this subject (such as Fletcher & Michener, 1987; Hepper, 1991). Among the fundamental tasks for the understanding of the social articulations of the organisms is the description and investigation of the mechanisms allowing family and immunological recognition; however, this may not be offered as proof of inclusive fitness; even more when there are clear benefits for the Darwinian fitness of these organisms. For example, the fact that workers distinguish their kin in the hive has a clearly adaptive value against the invasion of the colony by parasites and foreigners. As well, behavioral differences between individuals with differing degrees of kinship within the colony may be a non-adaptive by-product of inter-colonial recognition (Crozier & Dix, 1979; Carlin, 1989; Grafen, 1990; Alexander, 1991; see also Gadagkar, 1991a).

(2) If the individuals belonging to groups (family or not) with fewer "altruists" and more "cheaters" were less viable when compared with individuals of groups with greater proportions of "altruists", it would be possible to establish a certain proportion of "altruistic" alleles in the population due to "intra-group" and "inter-group" competition. Nevertheless, this explanation overlaps the group selection theory (Wilson, 1975; Wade, 1980; West-Eberhard, 1981; DS Wilson, 1983; DS Wilson & Sober, 1989; Bourke & Franks, 1995), and this is quite a good source of debate and misunderstandings.

Group selection is an idea that can be dated back to Sewall Wright in 1945, and after an intense period of criticisms, improvements and developments, it is beginning to be broadly recognized as something quite plausible and frequent in the natural world (DS Wilson, 1983). Its basic idea is that, when a large enough number of generations is considered, there might be a selection that disfavors not only less favored individuals, but also the less productive or less viable groups. Then, some features or behaviors that favor the whole group can evolve, even imposing an immediate cost on the individual. As these characteristics are not necessarily present in all the individuals of the group, we can model this situation in the perspective that there are many conflicting strategies in action. The terms "*altruist*" and "*conventional*", in this case, may be respectively translated to strategy "*benefactor of the group*" and strategy "*exploiter of the group*".

In each case, the nature of cooperation and the ecological conditions determine the minimum number of *altruists* necessary for the group to be efficient in maintaining itself or in generating "propagules". For example, Buss (1986) noted in the *Dictyostelium mucoroides* amoebae the need to group their disperse cells in order to form a reproductive body. Nevertheless, there is a certain

number of cells from parasitic lineages that never participate in the construction of the peduncle (the peduncle is the 'sterile' part of the amoebae). If this parasitic lineage (which is successful in the battle between cells to be reproducers) has a large representation when the reproductive body is going to form, it makes the process unfeasible. Thus, the coexistence of both cell types is made possible through the partial elimination of both by selection at the individual and group levels.

Even in families, if the spreading of altruistic traits is due to different survival or productivity of kin groups with different frequencies of altruistic traits (reviewed in DS Wilson, 1983; Bourke & Franks, 1995), then kin selection and group selection begin to be considered "*alternative ways of looking at gene frequency change in a population structured by relatedness*" (Bourke and Franks, 1995).

At the present stage this discussion could be merely a semantic one, and KS could be understood as a special case of group selection accepting these restrictions (Wade, 1980). But the KS theory (and group selection in some texts) claims to explain a broader range of phenomena, like the origin of eusociality or the existence of pluricellular organisms (*e.g.,* Hamilton, 1964; DS Wilson & Sober, 1989; Bourke & Franks, 1995).

Eusociality

The evolution of the eusociality is a fundamental problem covered by KS. As an example, the existence of non-reproductive bee workers is explained because of the great probability that the queen possesses the same genes which codify for the worker phenotype (altruistic condition).

However, other approaches which focus on developmental mechanisms can explain the phenotypic division of labor into reproductive and non-reproductive components starting from only reproductive ancestors. Defenders of KS admit the use of this kind of approach as an explanation for the beginning of eusociality, but not as an explanation for its maintenance (*e.g.,* Crozier, 1992). Contrary to this view, I will argue here that these theories can explain the appearance, evolution and maintenance of almost all the features related to the division of reproductive labor and colonial integration. On the other hand, it will be presented later that, where KS does need to be invoked, it is a group selectionist model that in reality is being used.

Phenotypic approaches to the evolution of eusociality

In some animals the older siblings simply devour the younger ones. This is the case of some cannibal beetle larvae studied by Eickwort (1973). What could be the advantages of such behavior? As explained by this author, in large broods where the probability of survival is low, this practice could significantly increase the chances of survival for the older siblings (thus increasing the net production of offspring by the parents).

Given the morphological, physiological and behavioral potentialities of many organisms, the distribution of tasks within the offspring may be much more sophisticated than the one resulting from the simple exploitation of one of the parties as food for another. In this way, Alexander (1974) and Michener & Brothers (1974) proposed an alternative explanation for the evolution of eusociality, called "Parental Manipulation". In this model, one part of the siblings may be 'employed' to help the other part of the progeny. In this way part of the progeny has an increase in its probability of survival that counterbalances (in terms of parental fitness) the reproductive lessening of the "slaved" progeny. Following this theory, altruistic behavior may evolve not due to the benefits awarded to the altruistic genes of the sacrificed progeny, but owing to the benefits to the "manipulative" genes contained in the parents.

The road that takes the individual from its zygote state until its reproductive state is adjusted by a multitude of genes that activate or deactivate other genes codifying discrete traits of the total ontogenesis. The expression of these genes - or even some phenotypic features - may be modified by the interference of environmental conditions (Smith-Gill, 1983; Buss, 1987; Bonner, 1988; West-Eberhard, 1986). So, as the location of a cell is fundamental in embryonic development in order to cause differential genetic activation (from chemical cues in the environment), what defines the partition of functions in the progeny can be factors that "*include the amount and quality of food received as a larva or nymph, the amount of yolk received while still an embryo in the egg, the temperature of the nest, photoperiod, the presence or absence of pheromones from the queens or other colony members, and others*" (Wilson, 1979 in revision of Wilson, 1971, Schmidt, 1974 and Lüscher, 1976; see also Bonner, 1965). This unequal distribution of phenotypes may also result from a process that

is generated automatically within the progeny as a result of the interactions among the members of this same progeny (*e.g.,* by dominance; Wilson, 1971; Michener, 1974; Michener & Brothers, 1974; Brian, 1980; West-Eberhard, 1981; Wheeler, 1986; Myles, 1988).

In this way, if an ancient solitary bee had a progeny in which a mutation codified aggressive behavior towards sisters (through the emission of a new compound or aggression that inhibits the sisters' maturation or mating; see Brian, 1980), this bee may have eventually obtained a large advantage if her sisters had been inhibited by her in their sexual characters, but not in those related to the care for young, territorial defense, etc. Daughters of this "mutant" could also express this behavior, thus reproducing the phenomenon. Basically, what will determine who will be the inhibitor and who will be inhibited are stochastic factors (Wilson, 1971; Michener, 1974; Brian, 1980; Wheeler, 1986; West-Eberhard, 1989) which, for example, make the first ones expressing the inhibition factor to be the inhibitors, the remnant consequently being the inhibited ones. The important point here is that the mechanism of purely selfish competition seems to more easily generate control systems of caste expression[8].

On the other hand, the appearance of additional anatomical or behavioral features in individuals are not requirements for the evolution of sociality since, for instance, "*The apparatus already possessed by the non-social bees was adequate to permit social evolution*" (Michener, 1974). Thus, counting on only one evolutionary innovation (or even, what is more probable, pleiotropic effects and contextual shifts, West-Eberhard, 1987) and with no need for any kind of altruism, it is possible to take the first step towards a system with condition-sensitive alternatives that results in functionally differentiated components (*epigenetic theory* of West-Eberhard, 1987, 1988, 1992) – which is a truly extraordinary fact. This means the

transposition of the limits of the individual organism to the "super-organism" articulated with different individuals. As several authors have pointed out (*e.g.,* Perrier, 1880, *apud* Boardman *et al.*, 1973; Jacob, 1970), this overlap is the basis for the articulation of much of the complexity of the organisms.

Towards the consolidation of eusociality

The relative isolation supplied by the genetic complexes differentially isolated by environmental conditions (illustrated by the alternative train tracks, Waddington, 1940 *apud* Gilbert, 1994) must also be a focus of attention. For example, in the development of an organism, cells that are determined to belong to the somatic lineage may, quite naturally, activate "suicide" genes (*e.g.,* Kirk, 1988). Similarly, modifications in a caste do not necessarily interfere directly in the ontogenesis of the other caste[9] (even though, depending on the case, they might) (West-Eberhard, 1987,1988[10]). As pointed out by Bonner (1965), "*If the steps did not occur in blocks or units that can be shifted or altered in toto without seriously affecting the rest of the organism, evolutionary change in a complex organism might have been virtually impossible*".

There is some kind of "determination point", as it is known in embryology, or "decision point" (*e.g.,* Hölldobler & Wilson, 1990; Noirot, 1990) for castes of insects, that is responsible for the distribution of phenotypes through the activation of different gene complexes, leaving these phenotypes relatively isolated from each other. This relative isolation also allows us to infer that the signals for one caste may not have an effect on the other castes. Thus, contrary to what is supported by Keller & Nonacs (1993), it is not necessary for the royal pheromones that are

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[8] One example that can be illustrative is the case of the primitive eusocial bee *Lasioglossum zephyrum*. Michener and Brothers (1974) observed that the queen is the most specialized one, and the specialized tasks of the workers are in fact what remains after the reduction of this activity by the queen: "*This specialization of the queen is likely to have resulted from her acquisition, along with the onset of eusocial behavior, of the ability to control workers. If the major leading to the appearance of a worker caste had been altruism, one ought to find evidence of it, other than reduced ovarian size and reduced frequently of mating which could both result from queen control*" (see also Wheeler, 1986; Wcislo, 1997b).

[9] Interrelated processes in the development such as heterochrony and pleiotropy are not being ignored. It happens that we are herein emphasizing the processes that allow the choice of the activation of the different genetic pathways. These activation processes obviously are in each case limited (or potentialized) by interference nets in the development.

[10] West-Eberhard (1988) also points out that the mutations that improve the task of the workers give the opportunity for kin selection to begin to act. As she defended in the same paper, the mutation will "*occur in a prolific female rather than in a reproductively or socially handicapped one*". Then, this female and the whole eusocial entity that she generates (when all parts of their life cycle are expressed) will have an increase in her Darwinian fitness. In this way it is difficult to see why this situation makes it easier for kin selection to begin to act.

distributed throughout the colony to have a physiological basis to act upon the emitting queen herself. This is because there may be differences between the queens and the workers that range from differences in receiving the message (receptors with different sensitivities. See also Nijhout & Wheeler (1982) for differences in the response after the decodification of the same information. Furthermore, social interactions frequently continue to operate as "inductors" of roles within the colony, even in advanced stages of the life cycle of individuals.

Certainly, the determination point must be found –preferentially– before individuals acquire the capability of reproduction. For example, in hactiline bees (Yanega, 1989, 1992 *apud* Crespi & Yanega, 1995) and polistine wasps (Mead & Gaboriaut, 1993 *apud* Crespi & Yanega, 1995), the castes are determined in the very first days of adulthood, before breeding starts. This idea would be consistent with the proposal that the term "eusociality" must be defined more explicitly, based strictly on the presence of castes[11]. As observed by Crespi & Yanega (1995), "*once an individual has entered a caste, natural selection of its behavior has become circumscribed in its effects to modification within a specific, limited range of behaviors. We believe that such specialization of behavior evolves only under selective conditions substantially different from those that have produced non-eusocial systems, and has profound evolutionary effects, and that elucidation of such conditions and effects is one of the main tasks of studies of social behavior*".

From the three conditions commonly required for an organism to become eusocial –overlapping of generations, cooperative care of young and division of breeding tasks (Batra-Michener-Wilson classification; Wcislo, 1997a)– it is only necessary to invoke the last one, since it represents the exceeding of what is fundamentally a physiological and evolutionary limit (and a "*discrete and historically recognizable event*" (Danforth & Eickwort, 1997). The other conditions are favorable factors, but are not irreplaceable in this process, and otherwise exclude clearly eusocial phenomena such as the soldier larvae described in parasitic wasps (review in Cruz *et al.*, 1990) or the sterile soldiers of aphids[12] (Itô, 1989).

Genetic differences among the components of an eusocial colony

We noted that the differences that make one component (be it a cell of an organism or a bee from a hive) become part of the breeding or sterile lineage do not stem from genetic differences, but from a differentiated expression of the same (or similar) genetic background[13] (West-Eberhard, 1988). The individual that is inhibited in reproduction ceases to exist as an individual concerning its reproduction in the same way as if it had died. But interesting things can happen in this process and all its subsequent history.

Starting again from a hypothetical scenery of the emergence of eusociality, this time imagined by Crozier (1992): "*Consider two wasps with cells side by side. Each has just laid an egg in her cell. One reaches over and eats the egg in the other's cell and replaces it with one of her own*". As we have seen before, this new behavior may confer a larger net offspring on the performer –because, for instance, the usurped wasp, who may simply not react to the aggression (Wcislo, 1997b), will continue to defend the nest and bring food to it. Furthermore, both wasps can be there side by side because in this species they remain in the maternal nest (*e.g.,* Wilson, 1971; Brian, 1980; West-Eberhard, 1981), and then the usurper's daughters (that lay eggs also in nearby cells) can also reproduce this system. Then we have the emergence of an eusocial colony.

However already at the beginning of this system, Crozier (1992) considers a possibility that in fact threatens all social system: "*Will selection favor genes predisposing the aggrieved party to*

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[11] Castes, according to the authors, would be the groups of individuals that became irreversibly distinct regarding their behaviour at some point prior to their reproductive maturity.

[12] It's curious that Stern & Foster (1997) do not consider that the aphids case can be included into de Crespi & Yanega's definition of eusociality because it implies "*potential conflict among colony mates arising from genetic heterogeneity*". Conflicts among colony mates can really have an important role in the formation of castes, but I was not able to note that genetic heterogeneity is involved in the process presented by Crespi & Yanega.

[13] Kerr (1950) described an interesting exception to the environmental system of caste determination. Actually, in the genus *Melipona* of the stingless bees, the caste determination has a genetic character: the queen phenotype is expressed by the presence of two loci in heterozygosis, and the workers' phenotype is expressed in the remaining cases. In this way, the eusocial system "found a way" of producing part of the progeny fertile and part sterile, with environmental stimuli having only a secondary role (Kerr & Nielsen, 1966).

retaliate?". His answer (in the case of interactions being among kin) is based on KS, considering that individuals that do not retaliate could be analyzed as containing altruistic genes. Therefore, these individuals would act differently depending on whether the usurper and usurped wasps are sisters, or daughter and mother, because they share different relatedness in each case.

But, contrary to KS, we do not need to investigate how this "altruist gene" could spread through the adoption of a different behavior toward different kin depending on the degree of relatedness. What we really have to search for is in what way the eusocial system is a strategy superior than the solitary one, because we can consider that "*eusociality is a discrete and heritable trait, which evolves by descent with modification*"[14] (Danforth & Eickwort, 1997). In an extreme view, individuals that retaliate or resist the pheromonal inhibition (or whatever nature of the inhibition) would have two effects: in the first place, the presence of these mutants among the progeny represent a "deregulation" of the division of labor. Therefore, depending on the number of these individuals, the incipient or advanced colony could be immediately destroyed. The other effect would be that the mutant descendants would no longer reproduce the colony organization, since there would be no way to inhibit part of its progeny to cooperate.

In both cases the system would be damaged, and, if the colonial organization has an adaptive value superior to the solitary organism, the mutation of the rebellious progeny will tend to disappear in a way analogous to the way a mutation of a rebel cell (cancerous) tends to be eliminated in pluricellular beings because this mutation generally damages strongly the organisms possessing it (Alexander, 1974; Bonner, 1988). The opposite case, therefore, in which there is a

regression to an individual organism, is also expected, when the latter is a superior strategy. Thus, within the allodapine bees, there is strong evidence of advent and regression of the eusocial condition because of environmental factors (Michener, 1974).

There are also intermediate situations. Different levels of "retaliation" can be supported by the colonial organization (also coexisting into the same colony). For instance, there may be "reproductive opportunities" for elements that have their function "determined" to be non-breeding components within the colonial structure. By taking advantage of these opportunities without harming inter-colonial selection (or even benefiting it), these features can be fixed. They can emerge in the following ways:

(1) Strategies such as "*exploiter of the group*", in the sense of the group selectionist approach exposed before, may appear since individuals make profit of the "group structure" of the colony (see Hillesheim *et al.*, 1989 for the interesting case of egg-laying and "lazy" workers of *Apis mellifera capensis*). However, it is important to emphasize that an organism (or eusocial colony) cannot depend on the encounters of different strategies (or alleles) to form a whole entity. If the eusocial colony of these bees –or the reproductive body of the amoebae previously mentioned– has some integrity and functional unity, it is certainly not due to the presence of two genetical strains of bees or cells, but due to the expression of a developmental program in the bees or cells, which generates the entity differentiation.

(2) As a complementary way of production of sexuates. In a Brazilian stingless bee species *Scaptotrigona postica*, the egg of a future drone is deposited by the workers usually inside a cell where the queen previously laid another egg. The drone larvae (larger and more active) devours the one that would develop a female[15] (Beig, 1972). This phenomenon acts as a very interesting strategy for sex ratio production in this species. Here, there was the introduction of an "egotism" regarding the male production by workers, that can however be assimilated into the colony system because it is possible to regulate this event without collapsing the colony reproduction. Potential reproduction of workers may also be maintained because it is very favorable as a reproductive stock in cases

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[14] An important consequence of what has been seen about eusociality up to now is that the whole phenotype contained in the genetic background of the organism must be expressed through the entire life-cycle not in one individual, but in several ones (West-Eberhard, 1986). This must happen in a coordinated manner by intrinsic mechanisms, which makes it an evolutionary and functional entity that will have to prove –like any other– its viability and reproductive efficiency in the environment. This entity has its unity granted not simply through common descent (*e.g.*, as in the case of the "evolutionary individual" that Janzen, 1977 identified in clones of aphids), but through a relationship between the parts that are functionally integrated. We also have not only to pay attention to the "extent" of the organism but also to consider a reasonable number of generations for the analysis of the fitness of the traits (Alexander, 1974).

where the colony loses its queen (Alexander, 1974).

However, it is also possible that in some cases the egg-laying by workers does not have a greater adaptive importance nor is it too harmful to the colony in the observed frequency, not having selection either for or against its maintenance within certain limits. Anyway, we always have to compute that there is also a strong selection over the dominant component (the queen) to overcome the possible "rebellious" mechanisms appearing in the worker caste, since the strengths of the system may be of great adaptive value. This introduces us to the next topic.

Why are most eusocial colonies monogynous?

According to all evidence, monogyny seems to be a primitive condition in eusocial organisms (Rosengren & Pamilo, 1983 *apud* Keller & Vargo, 1993). The queen and the drones are usually the components engaged with the genetic transmission in the system, and therefore represent the "germinative lineage". The position of the queen (and also the position of the king in Isoptera) occurs, as we have seen, by the "conquest" of this characteristic imposing to all others the condition of subordinates, through pheromones, battles, etc. In this sense it is an essential condition that the queen be as "egotistic" as possible, since if she grants "concessions", these concessions may be exploited by other "egotistic" individuals. This is in agreement with empirical data showing that "*reproductive competition is the major regulatory force of the reproductive roles, being amply mediated by the aggressive interactions*" (Keller & Vargo, 1993; see also West-Eberhard, 1981). This type of explanation radically differs from the explanation usually found in the literature, which regards the tendency towards monogyny among the advantages for the workers inclusive fitness (*e.g.,* Hölldobler & Wilson, 1977; Keller, 1993).

In this sense we often find that the "relaxation" of dominance that results in polygyny occurs when competition between colonies imposes tolerance between dominant individuals –even between unrelated individuals, and also even if these associations are less stable and finished as soon as possible (Hölldobler & Wilson, 1990). Therefore we have (1) a tendency toward monogyny

produced by internal competition, since the females that defeat their rivals will be more successful, and (2) a tendency to polygyny given by inter-colonial competition. As to the latter, for example, Wilson (1974) suggests that in *Leptothorax curvispinosus* ant colonies, the tendency towards polygyny would occur because the colony with many queens has a higher chance of survival, both in its establishment and in later stages, and also because queens may obtain advantages by living longer and producing more workers.

It is significant that most behaviors may be understood as favoring the maintenance multiplication of the colony, except those that are derived from conflicts for hierarchical "upgrade" within the colony (or also those destined to parasitize the colony, in the group selectionist sense). Therefore, what moves the colony is the selfishness of the breeders, limited by the viability of the colony. Several authors (*e.g.,* Nowak *et al.,* 1995) suggest the appearance of multicellular beings as the fruit of the cooperation between cells, their minor units. The line of reasoning presented here goes in the other direction: egotism and oppression between these minor units are a more prolific source than cooperation in the articulation of more complex structures.

Why don't we frequently see a direct inhibitory process in the sterile units by the fertile ones?

It is certainly correct to observe that neither pheromonal nor direct aggression from a queen would be efficient, for example in large colonies, in the case of a conflict of interests between the queen and subordinates. For this reason the pheromones would then act as honest signals, informing other members of the colony that the queen is present and active (Keller & Nonacs, 1993). We often see that the "policing by workers" (and not the pheromones and royal aggression) is an efficient means of controlling egg-laying by other workers in colonies with a queen (Ratnieks & Visscher, 1989). This is interpreted in agreement with the KS theory since workers may increase their inclusive fitness in this way.

Still, we may observe this same phenomenon as an improvement on the mechanism regulating the colony. The primitive systems of caste determination, based for instance on aggression, may be complemented (redundancy confers stability) or even substituted by other different systems once there has been a state of

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[15] Again, it is not possible to argue parsimoniously here in favor of an "altruistic" gene in the female larva which allows her to become food.

differentiation and integration (Wilson, 1971; Velthuis, 1976; Zucchi, 1993). Just as Bourke (1994) points out, *"it is unclear why caste determining and worker inhibition effects of queen's pheromone cannot be decoupled, if this serves the queen's interests".* Once the colony's cohesion is at an advanced state of eusociality, we have the possibility of exploitation of the royal pheromone for other functions, since the original function, related to division of castes, may now be accomplished efficiently by alternative methods. As an example we could mention the transition from a "pheromonal queen control" to a "pheromonal queen signal" (following the nomenclature of Keller & Nonacs, 1993). Thus, beginning with the message signaling the presence of the queen, which is transmitted to the rest of the colony, the policing by workers is a simple and elegant means of reinforcing the reproductive inhibition of workers through their mutual behavioral interactions.

In more extreme cases, when the queen would not be able to have a direct influence on caste determination –as in sibling associations that take place upon the death of the queen - the production of differentiated phenotypes in the progeny may continue to be done (or regress to this condition) by external environmental conditions (temperature, food, etc.; see Wheeler, 1986) or even through the individual interactions. As previously exposed, this can be done without the parents' influence for anything more than the genetic programming of the mechanism to activate or deactivate distinct genetic complexes according to all these environmental signals.

What makes the appearance of the eusociality more likely?

Wilson (1971) noted that eusociality appeared many times in the Hymenoptera, which is a remarkable fact. The explanation brought by KS was the "Haplodiploidy Hypothesis" (West-Eberhard, 1975) in which, due to the situation of haplodiploidy of the Hymenoptera, the sisters would be more similar genetically among themselves (r =) than to their mother (r = °), thus predisposing altruism among sisters because the genes that codify for altruistic behavior must have a greater probability of fixation.

But the number of exceptions found in nature regarding this genetic predisposition has been considerable. Due to phenomena such as polyandry, polygyny, workers egg-laying and the overlap of many generations inside the colony, the

main genetic similarity between the performers and the receivers of the altruistic act is not easily found (*e.g.,* Wilson, 1971; Hamilton, 1972; Lin & Michener, 1972; Alexander, 1974; Queller *et al.*, 1988; Hölldobler & Wilson, 1990; Gadagkar, 1990, 1991a; Bourke & Franks, 1995; Crozier & Pamilo, 1996).

In view of this fact, it was counter-argued that, in the origin of eusociality the genetic conditions for the fixation of the altruistic gene would be found (Wilson, 1971; West-Eberhard, 1987), and thereafter, even with low kinship indexes, the workers would not abandon their altruistic condition because the work of the altruists would be very efficient and the cost of abandoning the hive very high (*e.g.,* West-Eberhard, 1975; Hölldobler & Wilson, 1990). Although this is not incoherent, and considering the plurality of possible situations, the problem is that many studies "testing" and "supporting" the theory search for high indexes of kinship between altruists and beneficiaries and, when these high values are not found, these studies attribute very high benefits or very low costs to the altruist, depending on the situation. In this way, the analyses acquire a degree of arbitrariness that destroys the character of the model forecasting (they become "*ad hoc*" explanations).

This is even more stressed because when we seek for the degree of genetic similarity and the costs and benefits of the organisms in order to test the theory, we must clearly understand that we are not dealing with mechanisms by themselves (even though this confusion seems to happen in many studies). In reality, we are only facing a field of mathematical possibilities derived from Mendelian segregation laws that make the system of altruist-receiver relationships minimally able to be invaded by alternative strategies. In other words: when we find the conditions foreseen by KS, it does not necessarily mean that the genes codifying for altruism are present, but that the conditions exist for them to become fixed (and, seemingly, quite difficult ones if we take into account the criticisms presented along this text). Therefore, less favourable conditions are still a rather serious problem for the theory.

Anyway, the exuberant appearance of the eusociality in Hymenoptera deserves some explanation. Some authors (revised in Andersson, 1984; Hölldobler & Wilson, 1990; Alexander *et al.* 1991) mention certain phylogenetic and ecological potentials that are unique to Hymenoptera, such as the existence of strong

mandibles, stinger, and the frequent construction of hives, especially in ground aculeate wasps and bees. Also the help in raising the progeny would come from redirecting the already evolved maternal care of the adult female that is quite diffused throughout this group (Hamilton, 1964), also being a quite primitive characteristic of it on the whole[16].

In contrast, in the case of termites and naked mole rats (both eusocial, but not pertaining to Hymenoptera) that have a gradual growth, the young are miniatures of the parents (and not larvae) and already perform some of the functions of caring for the youngers (Alexander *et al.*, 1991). These authors suggest that as neither of the two sexes are pre-adapted for parental care when they are young, this behavior would arise together with eusociality, or as a part of it. Since the simultaneous appearance of different features is often difficult to conceive parsimoniously, we may imagine that in these groups the previous condition of young ancestors of both sexes –and which was used in the sterile castes– was the territorial defense of scarce resources (for cases of eusociality in shrimps living on corals, see Duffy, 1996; for Japanese aphids, see Aoki, 1977, 1982; Itô, 1989; and for Australian gall trips, see Crespi, 1992) tied to the tolerance by the immature in relation to individuals raised together (this immaturity is, as already shown, in a sense, "frozen" in the inhibiting process). In these cases, the "parental care" in the sterile castes of immature individuals could emerge later.

For their part, eusocial spiders present an interesting case in which growth is gradual. However, it is the female that is recruited for the sterile caste. This is due to the fact that here, too, the character already present in solitary species is that the females are those who spin the webs and defend them (and they may even present the parental care of regurgitating food for the young). This also results in a sex ratio in favor of a larger population of females among the progeny –in this case without the existence of haplodiploidy (Vollrath, 1986).

Finally, note that Thysanoptera, besides Hymenoptera, is an order that also shows

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[16] It is significant that in the eusocial beetle (Kent & Simpson, 1992), that also belongs to a holometabolic group, the adult is the one who is recruited. Furthermore, since it is the female that makes the holes in the wood and cares for the nest, it is specifically this sex that forms the sterile caste (noting that this occurs without haplodiploidy).

haplodiploidy, and males are also recruited for the sterile caste (Crespi, 1992). This comes to oppose Kin Selection, which foresees altruism only in female hymenopteran due to the haplodiploid system (Crespi, 1992; see also Saito, 1997 for the social Acari case).

Why is there an imbalance between sexes in Hymenoptera colonies?

Trivers & Hare (1976), in agreement with KS, understood that the probable reason for the existence of an imbalance between sexes in Hymenoptera colonies was the fact that workers in these colonies have a greater interest in the production of sister virgin queens, to whom workers share a r of 3/4, than in the production of brother drones, to whom they share a r of 1/4. Hence, an optimal investment on sex ratio would be 3:1 (females:males) in a randomly-mating population of colonies headed by a single and once-mated queen, and in which workers are sterile but have the sex allocation control.

It is certain that all these conditions vary between colonies, populations, species and other taxa where eusociality is found. In this way, it is possible to test Trivers & Hare's hypothesis, since in those cases where there is a departure from the situation described above (as in worker oviposition, polygyny, polyandry, or even when workers are partially or totally unable to control the sex investment) it would be expected an accordingly variation on sex ratio.

However, at the present stage, it is not possible to use the available data neither to confirm Trivers & Hare's hypothesis, nor to rule it out. This becomes clearer if we think in the many ecological and phylogenetic factors involved on sex ratio production, and in the amount of competing (or complementary) hypotheses which can also be invoked in each case (*e.g.*, Bourke & Franks, 1995; Crozier & Pamilo, 1996; Choe & Crespi, 1997). For example, we can understand the frequent imbalance toward females simply as a consequence of the phylogenetic constraints on the haplodiploid system of sexual production. In fact, as pointed out by Michener (1974), "*Evolution of sex ratio is, of course, bound up with the social evolution in hymenopteran societies where workers are females and produced in greater numbers and at different seasons of males*". Going further, the less biased sex investment toward females found in polygynous colonies could be explained by the fact that, as in these colonies the queens do not know whether her daughters will be made into workers

or breeders, the best strategy would be to produce a few more males that, certainly, will not be converted into sterile individuals. Nevertheless, this field still remains too open and, as exposed above, at the present stage we are far from considering sex ratio production as a test of KS.

Conclusions

KS certainly had a unifying role in the investigation of many evolutionary questions. Some authors received it so enthusiastically that one of its greatest defenders even wrote that "*If you accept the genetical theory of natural selection, as all serious biologists now do, then you must accept the principles of kin selection*" (Dawkins, 1979). But, in spite of the importance of KS, Dawkins's conditional sentence is not true. As expressed more accurately by Bourke & Franks (1995) "*Kin Selection is a logical corollary of gene-centered natural selection*", and not necessarily *all serious biologists* accept "gene-centered natural selection" (in the sense of Dawkins, 1976) as they accept "natural selection" (Gould, 1984). On the other hand, even accepting the logic of the gene-centered natural selection, we find some problems regarding the explanations given by KS to the appearance and maintenance of altruistic behaviors, since:

(1) In reality these behaviors are not "altruistic", because they are favoring directly the performer as an individual that aims to maximize its progeny (computing the effect of the expression of the behavior in its whole life cycle and in that of its progeny);

(2) these behaviors can be considered as strategies resulting in a benefit to the group, being maintained by the different survival or productivity among groups - and they can be handled into the scope of the group selection theory;

(3) they can be considered as task by-products of a developmental system composed by many "individuals" performing different tasks (the genetic information under selection is the one responsible for the multiplication and subsequent differentiation of subunits).

Another kind of problem (external to the theory, but affecting its study) is that as a good scientific hypothesis, KS provided us with criteria which allow us to test it objectively (prevision of degrees of relatedness, kin recognition, sex ratio), but data obtained in many studies, even being not favorable to KS previsions, are interpreted in such way.

In 1975, Wilson published a sociobiological synthesis that placed ideas in this field that would be discussed in the next twenty-five years. This synthesis had the goal of seeking for laws that would unify the behavior of phylogenetically very distant groups. The stated central problem was altruism, and the responses generated at that time were KS, reciprocal altruism and mutualism[17]. But, in spite of the Kin Selection's undeniable originality and heuristic contribution, the problems that it faces guide us to doubt it as the "ultimate cause" underlying altruism in situations normally referred to.

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[17] In the current text, issues like mutualism and reciprocal altruism were not discussed, since they usually have no interference on the KS debate.

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