Ann. Zool. Fennici 38: 239–254 ISSN 0003-455X
Helsinki 10 September 2001

Dedicated to the memory of William Donald Hamilton

A life-history approach to group living and social contracts between individuals

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Received 11 January 2001, accpeted 18 April 2001

Nonacs, P. 2001: A life-history approach to group living and social contracts between individuals. — *Ann. Zool. Fennici* 38: 239–254.

A social behavior continuum from simple to complex is argued to be a basis for evolutionary categorization of species. I propose a complimentary view that compares similar life history decisions because social complexity varies in many species across their lifetimes. I specifically concentrate on the evolution of reproductive skew in cooperative breeding, which I define relative to the ability of group members to live solitarily or move easily between groups (i.e., facultative versus obligate eusociality). Facultative cooperation can arise through social contracts based either on conventions (arbitrary asymmetries determines status), or transactions (individuals cede benefits for group stability). These mechanisms predict different within-group dynamics. An analysis of transactional models predicts eusocial evolution requires large asymmetries between dominants and subordinates in ability to succeed independently. The only major exception appears to be cooperative colony initiation by polistine wasps. Their behavior, however, may have evolved due to a unique combination of reproductive gains through sex ratio conflicts with workers and factors that select for reproductive plasticity in offspring. Examining eusocial evolution as a specific life history trait also suggests that facultative versus obligate cooperation correlates with assumptions about dominant control over skew within groups. 'Concession' type models tend to predict behavior in facultative situations, while 'Tug-of-war' models do better in obligate situations.

Levels of social behavior

William D. Hamilton was arguably the single greatest student of social behavior. He made seminal contributions towards understanding why grouping can be intrinsically beneficial (Hamilton 1971), why groups may be predisposed to form along lines of genetic kinship (Hamilton 1964), and why kin groups can still be considerably fractious over such matters as

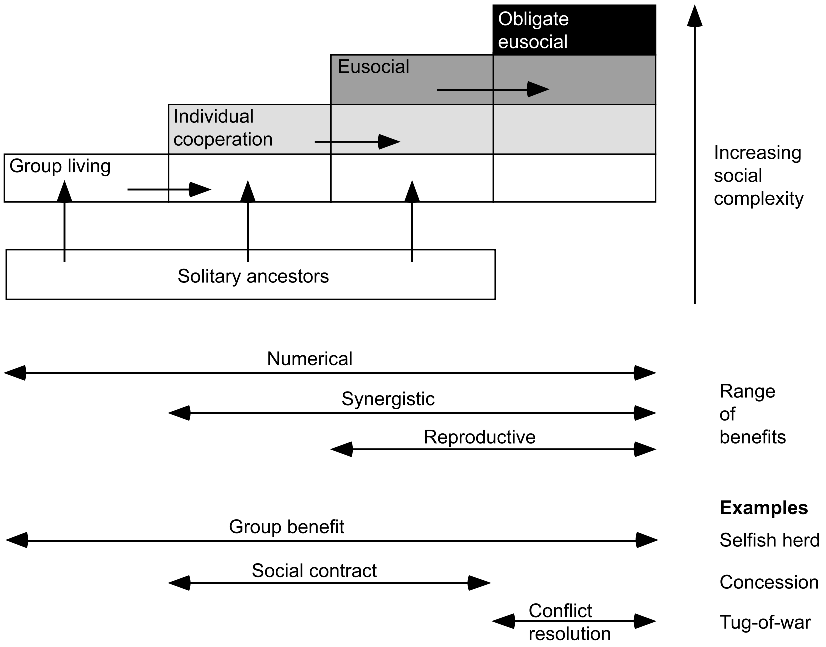

Fig. 1. The levels of sociality, the range over which several types of benefits can accrue, and the type of evolutionary models that are applicable. Social organization is represented as five levels of increasing complexity. Each cooperative level can have added benefits that are absent in the immediately lower levels. For example, a Eusocial group may enhance its productivity through behaviors that increase numerical, synergistic and reproductive benefits. Obligately Eusocial groups may even further enhance productivity through the evolution of morphological castes. Evolutionary transitions (indicated by arrows) can lead from solitary ancestors to either Group Living, Individual Cooperation, or Eusociality. Eusociality can also evolve from Individual Cooperation, which in turn can evolve from Group Living. Obligate Eusociality, however, can evolve only from Eusociality.

offspring sex ratios (Hamilton 1972). In this paper, I will give a broad overview of how all social behavior can be viewed as layers of increasing behavioral complexity which determine how conflicts are resolved. I will specifically concentrate on how ‘social contracts’ may be struck between individuals in which cooperation is a facultative decision. In particular, I will suggest that polistine wasps are both an ideal system in which to test social contract theory, and also socially unique in ways that illustrates the preeminent role of ecological constraints in the evolution of cooperative breeding.

At one end of the social spectrum are species that form anonymous groups in which all individuals are functionally equal, no individuals have specific roles or duties, and there is no significant individual identification (Fig. 1). A particular example is anchovy fish. Anchovies form schools that can be as large as several million individuals (Nonacs *et al.* 1994). Within a school, however, there are no leaders or dominants and no fish individually recognizes or specifically interacts with any other fish. Within the group, reproduction by any given individual is limited only by its feeding rate. At the other end of the spectrum are species in which group members have specific roles that require distinct identities. Roles are so circumscribed that no individual can do them all (i.e., no individual is totipotent) and many individuals develop or take roles that lead to sterility. Therefore, reproduction is obligated to occur in groups. An ant colony is such a society. One or several individuals are reproductives (the queens) and the rest are generally sterile brood tenders or foragers (the workers). In more elaborated species, the workers themselves come in various sizes and shapes, with each caste having some preferred work specialization (Wilson 1971). In the middle of the spectrum are species where there is active cooperation between individuals towards territory defense, prey capture, and reproduction. I delineate, for reasons discussed below, between groups where reproduction is not a cooperative endeavor from those where it is. Individually cooperative groups, such as a flock a pelicans diving in unison at a fish school, gain more food individually by cooperating but do not reproduce as a group. Eusocial species, like polistine wasps or wolf packs, can gain through both cooperative defense of nest or territory and coordinated reproduction. However, reproductive success may often be skewed within the group to favor those that are behaviorally dominant (Reeve and Keller 1995, Brockmann 1997).

The groupings presented here are an elaboration of the eusociality continuum suggested by Sherman *et al*. (1995). This continuum considered only groups with cooperative breeding, and as such is criticized as implying that non-breeding groups are therefore behaviorally simple and uniform (Costa & Fitzgerald 1996). The framework here is thus more inclusive. I also maintain a separate category of obligate eusociality based on totipotency of individual group members (as in Gadagkar 1994). From an evolutionary perspective, the expression of cooperative behavior may be strongly influenced by the degree to which subordinate group members have options for switching between groups or for living solitarily (Crespi & Yanega 1995, Johnstone 2000, Magrath & Heinsohn 2000).

Obligate group living, *per se*, does not always lead to reproductive skew and loss of totipotency. Many species may only be found in groups where individuals exhibit no defined roles. For example, any individual anchovy is totipotent and could theoretically live solitarily, but mortality rates on individual fish are so high that functionally none survive apart from a group (Blaxter & Hunter 1982). A solitary life is no more a realistic option for an anchovy than is a solitary life for a worker ant. Group-living, individual cooperation, and eusociality are therefore not necessarily unique character states where the appearance of the former must precede the latter (Fig. 1). A fully eusocial species can evolve directly from a solitary ancestor (e.g., within wasps: Carpenter 1991). Only obligate eusociality is difficult to imagine evolving from any other state than existing eusociality.

Sociality can be defined on the hierarchy of benefits that may accrue to group living organisms and the type of models that may apply to each type of social organization (Fig. 1). The simplest benefits are numerical in nature and increase with group size. Groups have more eyes to see predators or prey. If attacked by a predator there may be confusion effects or a reduction in individual risk by having nearby conspecifics that attract the predator. Groups may have aerodynamic benefits for flight or swimming. All such benefits can accrue without individuals deciding to specifically help any other particular individual. So in anchovies it is imperative for the individual to be a member of a group with similarly-sized individuals. It is almost immaterial to which group a fish belongs and even groups containing non-conspecifics (e.g., sardines) would be acceptable (Blaxter & Hunter 1982). The next level of benefits is synergistic in that they demand individually-coordinated activity for a task that may be impossible for a single individual. Examples would be cooperative hunting for large prey in carnivores such as wolves or lions. Similarly in ants, a group of foragers can retrieve items far too large for any single forager to collect. Group or individual recognition is likely to occur, but is not a specific requirement. Group membership would therefore exhibit stability over time and specific rules for admittance, retention, or exclusion could evolve.

For group living or individual cooperation to be adaptive, numerical or synergistic benefits must be such that they eventually translate into increased inclusive fitness. Individuals will vary in their reproductive success, but only through environmental variability and chance events. Reproduction is neither directly suppressed nor enhanced by the actions of group mates. If the reproductive success of an individual is both a function of the experienced environmental variability and the behavioral dynamics within the group, then the organization level can be considered as eusocial. Two features are often found in eusocial groups. Groups produce more offspring that solitary individuals and reproductive success is likely to be skewed such that some group members consistently do better than others. The variance may be such that subordinate individuals in highly productive groups actually reproduce less as group members than could be expected as solitary individuals. Thus evolutionary models based only on numerical or synergistic benefits for productivity may be inadequate to explain the decisions of subordinate group members.

Models of synergistic and reproductive benefit

It is important to note that the sociality spectrum described here can apply to a species entire life history or vary across its life history. For example, anchovies are always group living and at no point in their lives exhibit individual cooperation or eusociality (Blaxter & Hunter 1982). On the other hand, in polistine wasps different parts of the their life cycles have differing levels of social complexity (Gadagkar 1991, Reeve 1991). Temperate polistine wasp species, such as *Polistes dominulus* and *P. fuscatus*, are particularly good examples. Mated females overwinter together in hibernacula (West-Eberhard 1969, Turillazzi 1980). Any potential benefits to result from such an aggregation are likely to be entirely numerical because the wasps neither reproduce nor collectively build and defend any structure or territory. Thus, this behavior is most likely an example of group living. Upon emerging in the spring, foundresses may or may not collaborate in nest initiation (Reeve & Nonacs 1992, Nonacs & Reeve 1995). In collaborations, one female becomes dominant and lays the majority of eggs (Reeve *et al*. 2000), which fits with the definition of eusociality. When the brood matures, some of the offspring decide not to mate and become workers, thereby sacrificing their totipotency (Reeve *et al*. 1998b, Starks 1998, 2001). Thus the relationship between the foundress and her workers is obligately eusocial. Finally males in some species form mating leks or release pheromones jointly to better attract females (reviewed in Beani 1996). This could fit with a definition of individual cooperation.

Group living

Group benefit models generally postulate that, *per capita,* either predation risk must be lowered or foraging gain increased for group living to be adaptive (Alexander 1974). There are obviously many ways that either can be achieved. Consequently no general model of sociality has been proposed, although specific types of numerical benefits have been treated mathematically. Some examples are the propensity of individuals to hide behind others (the selfish herd: Hamilton 1971), levels and benefits of vigilance for group members (Lima 1995), and reductions of foraging variance with larger group sizes (Wenzel & Pickering 1991).

Facultative group living and social contracts

Layered upon numerical benefits are synergistic and reproductive benefits. A logical assumption is that the behavioral mechanisms required for such interactions could not have evolved unless their possessors had fitness advantages. This does not imply, however, that these benefits have replaced numerical benefits. Instead these behaviors may evolve as further adaptations that increase the already present numerical benefits of group living. I suggest that adaptive models for within-group interactions fall into two categories: (1) Social contract models; and (2) Conflict resolution models. The suitability of each model-type depends primarily on the degree of freedom that apparent ‘losers’ of within-group struggles have to switch groups or to live solitarily (Fig. 1). The social contract models apply wherever alternative options are present, conflict resolution models apply whenever such options are absent.

I define any situation where there is both individual cooperation and a realistic opportunity for subordinates to either switch groups or live solitarily as a social contract. In essence this simply describes situations where cooperation may or may not be offered, and where cooperation may or may not be accepted. The rules for whether particular individuals can form a stable group are either: (1) Conventional, where an accepted asymmetry determines each member's role and behaviors; or (2) Transactional, where each member's role is 'negotiated' relative to its physical attributes and alternative options. Because the concept of a social contract was first introduced in the context of transactional sharing of reproduction (Reeve & Nonacs 1992), they have been viewed as interchangeable (e.g., Field *et al.* 1998). However, 'social contract' should be the more inclusive term. Individual cooperation without reproductive benefits can be viewed as a social contract. Even shared reproduction may reflect a shared convention rather than a dynamic transaction. Given this last possibility, it is necessary to clearly distinguish between cooperation through a convention and cooperation through a transaction.

Conventions

Conventions can be based on any number of factors such as: order of arrival, size, age, parent versus offspring, level of genetic similar (actual or perceived), and resource holding potential. Logically these conventions should not be arbitrary but instead reflect a real underlying asymmetry in ability. Thus, if the conventions were to be ignored and roles were contested, either the asymmetry would hold true or the cost of contesting would exceed the potential gains for role reversal. Therefore a convention is roughly equivalent to a 'rule of thumb' that approximates the outcomes of the more sophisticated processes involved in transactional interactions. A possible example is in hyenas where females and males have sex specific dominance hierarchies, but females generally appear to be conventionally dominant to males (Kruuk 1972). The fact that males do not appear to seriously contest female dominance probably follows from females being larger, stronger and more aggressive. Within each sex, however, status and rank are more aggressively pursued with less respect to convention, as might be expected given that individual physical states and kin structure in the pack are likely to be highly dynamic.

Conventions might be favored, therefore, under environmental conditions where the viability of alternative options are poor or highly predictable, and the asymmetric character has a high correlation with winning contests. Conversely, transactional interactions should be found where within-group and environmental conditions are likely to be more dynamic. Moreover, both conventions and transactions might occur within the same social group. For example, in a eusocial group of birds, there might be a convention for males to never copulate with their mother under any condition, but to help raise her offspring. However, if an unrelated female replaces the mother, males may not help unless they become her mates (e.g., Emlen *et al.* 1995).

Transactions

Reeve and Ratnieks (1993) provided an inclusive fitness framework based on Hamilton's rule for predicting the joining decisions of individuals based on both subordinate and dominant gaining by cooperating. A subordinate will have fitness equal to being solitary, when:

$$k[p_{\min} + r(1 - p_{\min})] = x_s + x_d r, \qquad (1)$$

or:

$$p_{\min} = [x_s - r(k - x_d)]/k(1 - r), \qquad (2)$$

where r is the relatedness of the dominant to the subordinate, x_s and x_d are the expected reproductive success of breeding alone for the subordinate and dominant individual, and k is the reproductive success of a group of two. (Note that although this model is framed in a eusocial context, it could just as well apply to individually-cooperative groups where k and x can be other values, such as energy gained through foraging.) The maximum proportion a dominant is willing to cede is calculated as:

$$p_{\max} = (k - x_d - r x_s)/k(1 - r), \qquad (3)$$

where r is the relatedness of the subordinate to the dominant. An association can be stable where

$p_{\min} \leq p_{\max}$. Substituting Eqs. 2 and 3 into this equality and assuming symmetrical relatedness values, yields with rearrangement the potential stability condition of:

$$k \geq x_d + x_s. \tag{4}$$

Thus the difference between $p_{\max}$ and $p_{\min}$ is the range in which dominants and subordinates can negotiate reproductive skew. The actual realized skew is predicted to be a function of the relative control that dominants and subordinates have within groups (Reeve & Keller 2001). Total control by the dominant leads to a 'concession' model, where the dominant is predicted to give the subordinate close to minimum reproductive incentive needed to induce it from solitary life. If the subordinate controls its own reproduction within the group, then a 'restraint' model is suggested where the subordinate reproduces close to a maximum point that would trigger eviction from the group by the dominant. Shared control, leads to a 'tug-of-war' model, where the skew reflects each contestant's relative strength. The differences between these three versions of transactional models are more than semantic. The three models predict different sets of relationships between reproductive skew, relatedness, aggression, and the effects of ecological constraints on group and individual productivity (*see* extensive treatments in Johnstone 2000, Reeve & Keller 2001).

Obligate eusociality and conflict resolution

The general form of a transaction-type model can incorporate the entire range of assumptions about control within groups and is therefore applicable across both facultatively and obligately eusocial groups (Johnstone 2000). However, when a subordinate cannot realistically leave a group or a dominant's fitness would be severely impacted by evicting or killing the subordinate, then the explicit assumptions of the special cases of concession and restraint models are violated. Dominants, with total control, no longer have to offer any concession to retain subordinates. Subordinates, with total control of their reproduction, no longer have to show any restraint to prevent their expulsion. Conflict would be resolved by a tug-of-war that reflects each side's strength to contest (Reeve *et al.* 1998a, Johnstone 2000). If one side absolutely wins, the other must accept the result as a best of a bad situation. Thus, it may be heuristically useful to continue to use special cases of transactional models rather the general form.

Within obligately eusocial Hymenoptera there are several examples of conflict resolution between queens and their workers. Because of an asymmetrical relatedness to sisters and brothers, workers favor a female-biased sex investment ratio in opposition to the equal investment favored by the mother. Although exceptions exist, the balance of the data strongly suggest that workers are the greater 'winners' in this conflict because they control the feeding of the brood (Trivers & Hare 1976, Nonacs 1986, Bourke & Franks 1995). It is also to a worker's genetic advantage to replace brothers with its own haploid eggs. However, queens can 'win' this conflict by either multiply mating (which favors workers to police reproduction among themselves: Ratnieks 1988) or hiding the sex of offspring until late in development (Nonacs & Carlin 1990).

Bourke and Franks (1995), and Crozier and Pamilo (1996) provide excellent overviews of the theory behind various conflicts among group members within obligately eusocial species, and Reeve and Keller (2001) show how transactional models can be applied to resolving a number of these conflicts. Therefore, I will not further consider models of conflict resolution within obligately eusocial societies, but instead concentrate on the evolution and maintenance of facultative eusociality.

Group formation dynamics

There are two separate questions in how groups form. The first is what advantage does group living have over solitary living, and the second is by what proximate mechanism is group membership and role decided? The second question also has an ultimate component in the assumption that animals should use proximate rules that increase their fitness. Therefore for an individual to join a group (or similarly for any individual to allow another to join) it must gain fitness relative to staying alone.

Conventions versus transactions

Groups organized either by conventions or transactions should at an ultimate level reflect Hamilton's rule for each group member where benefits provided (weighted by genetic relatedness) exceed costs experienced ($rb - c > 0$). The proximate behavioral manifestations involved in group formation and stability could, however, be quite different (Table 1). Transactional models predict that both increased environmental constraints on success apart from the group and increased productivity benefits to cooperation positively correlate with stable group formation. Groups formed by convention should be largely insensitive to fluctuations in either parameter.

In a transactional framework, groups composed of close relatives should be more likely to form than groups composed of distantly or unrelated individuals (Reeve 1998). At a population level this would predict significant bias towards finding groups of relatives, but a key prediction of transactional models is that groups of low relatedness could be common. Wasp foundress associations in *P. fuscatus* (Reeve *et al.* 2000) and *P. dominulus* (Queller *et al.* 2000) appear to follow such a pattern. Conversely with conventions, genetic relatedness within groups should be uniform (if the joining convention is based on perceived kinship) or close to random (if the joining convention is not based on relatedness). Wasp foundress associations in *P. bellicosus* and *P. canadensis* therefore support a convention model in being highly uniform in relatedness although populations are composed of both relatives and non-relatives (Field *et al.* 1998, D. C. Queller pers. comm.). At the other extreme, in ant species where queens cooperate in initial brood rearing (pleometrosis), relatedness appears to play no role in structuring groups (Bernasconi & Strassmann 1999). Similarly, relatedness may play a minor role in wasps adopting worker or reproductive roles in *Ropalidia marginata* (Shakarad & Gadagkar 1995, Arathi *et al.* 1997).

Finally, in conventional groups actual competitive ability may not correlate with dominance rank (e.g., in *R. marginata* the reproductively dominant wasp is sometimes not the most behaviorally dominant: Chandrashekara & Gadag-

Table 1. Comparison of predicted responses by groups forming through social conventions or transactions to factors affecting the benefits of cooperative behavior.

Factors in transactional models	Conventional	Transactional
Increasing ecological constraints (*x*) for leaving group	No response	Increase cooperative behavior
Increasing group benefits (*k*) for cooperative behavior	No response	Increase cooperative behavior
Genetic relatedness (*r*)	All groups of similar or random relatedness	Groups mostly of close relatives, but with a distinct proportion of more distantly or unrelated individuals
Decrease in competitive ability of dominant	No response	Large effects on skew or dominance hierarchy
Predicted behavior in group		
Aggression levels	Low to absent	Variable to high
Reproductive strategy of subordinate	Reproduces only if dominant dies (hopeful reproductive)	Often reproduces in presence of dominant (optimal skew)
Overall group productivity	Higher	Lower

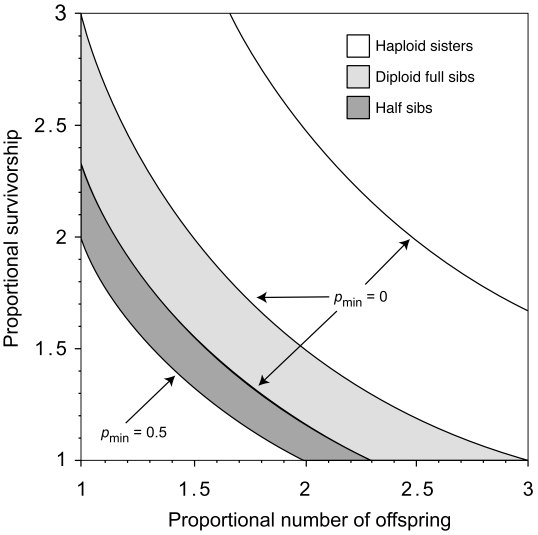

Fig. 2. The minimum group productivity (k) for subordinate behavior to be favored as a product of number of offspring and their survival to maturity. If reproduction is equally shared (p_{min} = 0.5), the minimum k, as a product of number and survivorship, for cooperation to be favored is 2 for all groups, independent of the relatedness between members. As reproduction becomes skewed towards the dominant, k must increase. The range of values for $0.5 \geq p_{min} \geq 0$ is shown for haplodiploid full sisters ($k \geq 2.33$ at p_{min} = 0; dark gray), diploid full siblings ($k \geq 3$ at p_{min} = 0; light gray), and half siblings ($k \geq 5$ at p_{min} = 0; white).

kar 1991). This latter point would further predict that aggression is low between dominants and subordinates because conventions do not require testing or reinforcement. Lower aggression, in turn, should positively affect group productivity. In contrast, key assumptions of transactional models are that hierarchies are contested and thereafter probed for weakness through manifest aggression. This continued aggression should reduce group productivity. Extending this logic predicts that the loss of group productivity may also be the ultimate factor in favoring the evolutionary replacement of transactions with conventions. Although aggression varies greatly across species and across nests within species of polistines (Gadagkar 1991, 1996, Reeve 1991), there has been no comparison of within-nest aggression to overall productivity to test this prediction.

Reproductive benefits versus ecological constraints

The stability condition given in Eq. 4 yields two predictions. First, social contracts are possible between any two individuals whether they are related or not. Second, if $x_d = x_s$ then the reproductive productivity (number of offspring × survival rate to maturation) of a pair equally sharing reproduction must be twice that of a single individual. There cannot be a *per capita* reduction in reproductive success within groups. Skew further increases the minimum k for cooperation for the individual expecting the smaller share in reproduction. With total skew (p_{min} = 0), k must be ≥ 2.33 for full sisters (r = 0.75) to cooperate. By similar substitution of values, for diploid full sibs to cooperate with p_{min} = 0, k must be ≥ 3. For half sibs, k must be ≥ 5.

Cooperation could conceivably increase k through increased offspring production (i.e., a direct reproductive benefit) or increased survival of offspring (i.e., numerical or synergistic benefits in nest defense against parasites, predators, or usurpers). Therefore, the minimum k needed for cooperation to be evolutionarily favorable can be calculated as a function of numbers and survivorship. In Fig. 2, I plot the combinations of increased offspring and survivorship for pairs of haplodiploid full sisters (r = 0.75), diploid full siblings or parent-offspring (r = 0.5), and half siblings (r = 0.25) that predict cooperation. The graphed areas represent the range as p_{min} goes from equal sharing to total skew for the dominant for the three levels of relatedness. Finally, I define $x_d = x_s = 1$, so that k is calculated as a proportional increase.

The curves illustrate the difficulty in cooperation evolving between two reproductively equivalent individuals. Assuming that reproduction is shared equally between the two individuals (the bottom solid line), cooperation has to increase either numbers of offspring or survival by a minimum of 40%. As skew increases ($0.5 > p_{min} \geq 0$) the benefits must increase for an individual to favor accepting a subordinate role. For the most favorable case of haplodiploid sisters, either numbers or survival must almost always increase by 50% or 60% for skew to be able to evolve to be 75% or 100% in favor of the dominant. For diploid full sibs or any half sibs, the needed gains become correspondingly and prohibitively large. In eusocial haplodiploids it may be argued that *k* values are high enough to favor the maintenance of cooperation. For example, in *P. dominulus* single foundress nests grow at a rate of 1.02 cells per day, while multifoundress nests grow 1.42 cells per day (Nonacs & Reeve 1995). The estimated nest survival to worker eclosion of single foundress nests is 61%–76% that of multifoundress nests (Starks 2001; H. K. Reeve pers. comm.). Taken together this suggests that *k* for *P. dominulus* is between 1.83 and 2.28. However, this estimate for *k* follows from a long evolutionary history where the gains from sociality have been adaptively shaped. At the first appearance of cooperation, it may be only in very special cases that *k* can be doubled or more. Furthermore, even the maximum estimate cannot account for cooperation between non-full sisters as observed in *P. dominulus* by Queller *et al.* (2000).

Therefore, transactional models strongly imply that reproductive non-equivalence ($x_d >> x_s$) is a needed prerequisite for the evolution of cooperation. Such non-equivalence can arise in two ways. First, by manipulating feeding regimes parents can produce some offspring whose success as solitary breeders is so low that they maximize their inclusive fitness by assuming non-reproductive helper roles. A relevant example may be vespine wasps where the difference between sterile worker females and reproductive females is nutritional (Greene 1991, Matsuura 1991). Thus, a queen in founding a colony can insure that offspring remain as workers by raising them in small cells and not providing enough food to grow large. Second, non-equivalence can result from strong ecological constraints. If nesting territories or access to food resources are limited and monopolized, then dispersing offspring of territory holders may be expected to have considerably lower expected reproductive success than their parents. In a review across vertebrate species, Brockmann (1997) found that cooperative breeding is almost invariably associated with some aspect of territory defense, food gathering, or nest construction. Potential dispersers are always faced with the loss of some substantial resource that may not be readily obtained elsewhere.

Polistine wasps as a model system for testing transactional models

Polistine wasps in temperate climates have been the taxonomic group where transactional models have been most intensely tested (Koenig & Haydock 2001, Reeve & Keller 2001). Therefore, it would be useful to review whether existing transactional models are sufficient to explain the origin of cooperation in this group as opposed to explaining the behavioral dynamics within existing cooperating groups (e.g., Reeve & Nonacs 1992, 1997, Reeve & Keller 1995, 2001, Reeve *et al.* 2000). To begin with, we need to consider whether subordinate behavior at the initiation of cooperation satisfies Hamilton's rule through a combination of reproductive gains and physical constraints.

Benefits and constraints

Upon emerging from hibernation, temperate polistine wasps can either join with other females to initiate nests (pleometrosis) or build by themselves (haplometrosis). As presented above, the lower limit of *k* being 2–2.33 for full-sister cooperation to be adaptive may not be reached even in species where cooperation probably has a long evolutionary history. Therefore, reproductive benefits alone are unlikely to explain the initial evolution of the trait. The alternative is that ecological or morphological constraints affect potential dominants and subordinates in differing ways, so that $x_d >> x_s$. This relationship could develop in two ways. First, there could be strong nest site limitations such that those wasps that appropriate the limited sites could force others to accept subordinate roles or not breed at all. However, the balance of evidence suggests only for perhaps a few species are nest site limited (Queller & Strassmann 1988, Strassmann & Queller 1989, Gadagkar 1991, Reeve 1991). Second, individuals may become subordinates because they are intrinsically inferior to dominants at being solitary foundresses (Gadagkar 1990). Several lines of evidence, however, suggest that there are not pervasive differences in reproductive capabilities of temperate wasps at the nest initiation phase. Large wasps are not better than small ones at building or providing for offspring as single foundresses (Nonacs & Reeve 1995), and subordinates within groups are reproductively capable as they readily lay eggs if opportunities arise (Reeve 1991, Shakarad & Gadagkar 1997, Field *et al.* 1998, Starks 1998, 2001, Reeve *et al.* 2000; but *see* Gadagkar 1990, 1996). Therefore if neither reproductive benefits nor ecological and morphological constraints can account for cooperation, there must be another factor involved. I propose that for eusocial Hymenoptera, this extra factor is sex ratio conflicts between foundresses and their workers.

Sex ratio conflicts and reproductive skew

Consider a population composed of haplometrotic foundresses (with singly-mated females). This sets up the classic parent-offspring conflict situation in haplodiploids where parents prefer a 1:1 sex-investment ratio, while their offspring prefer a 3:1 female bias (Trivers & Hare 1976). Data from several polistine species that are almost exclusively haplometrotic, exhibit significant female bias that is more aligned with worker optima than with foundress optima (P. Nonacs unpubl., data from Suzuki 1986, Spradbery 1991). Therefore, from the foundress standpoint, male offspring have higher reproductive values than female offspring (Crozier & Pamilo 1996). For situations where offspring vary in their reproductive value, I expand the transactional framework for cooperation in Eq. 1 to:

$$\begin{aligned} &k[(f_s g_{sd} n_F/F + (1 - f_s) g_{ss} n_M/M) p_{min} \\ &+ (f_d g_{dd} n_F/F + (1 - f_d) g_{ds} n_M/M)(1 - p_{min})] = \\ &x_s(f' g_{sd} n_F/F + (1 - f') g_{ss} n_M/M) \\ &+ x_d(f' g_{dd} n_F/F + (1 - f') g_{ds} n_M/M). \qquad (5) \end{aligned}$$

Following the conventions of Crozier and Pamilo (1996), values for each term can be calculated for foundresses in a population with a 3:1 investment ratio in females to males (Table 2).

If there are some multifoundress nests within the overall haplometrotic population, these foundresses can substantially increase their fitness by sharing in the parentage of wasps that will become workers. Given that these workers may not discriminate precise relatedness of the maturing brood (e.g., Strassmann *et al.* 2000), it follows that they should prefer more male investment than workers on haplometrotic nests (Trivers & Hare 1976). Indeed, both foundresses and workers on a rare multifoundress nest can 'agree' to maximize their fitness by producing all males in the sexual offspring ($f_s = f_d = 0$; Boomsma & Grafen 1990). Under such conditions, subordinate behavior is favored in a full sister if $p_{min} > (3.5 - 3k)/k$, or $k > 3.5/(3 + p_{min})$ even if the subordinate has the same expectation for solitary success as the dominant ($x_s = x_d$). If reproduction is shared equally ($p_{min} = 0.5$), then two foundresses are favored to collaborate if $k > 1$ (note that this condition holds across all levels of relatedness). For skew to be total between full sisters ($p_{min} = 0$), k need only exceed 1.167 because from the standpoint of the subordinate,

Table 2. The terms and their values in the equation for foundress cooperation in a population with a 3:1 investment ratio in females to males (values as in Crozier & Pamilo 1996).

Term	Symbol	Value
Relatedness to subordinate of own daughter	g_{sd}	0.5
Relatedness to subordinate of own son	g_{ss}	1
Relatedness to subordinate of dominant's daughter	g_{dd}	0.375
Relatedness to subordinate of dominant's son	g_{ds}	0.75
Female reproductive value	n_F	2
Male reproductive value	n_M	1
Population proportion of females	F	0.75
Population proportion of males	M	0.25
Proportion of reproductive effort invested in females by subordinates	f_s	0
Proportion of reproductive effort invested in females by dominants	f_d	0
Proportion of reproductive effort invested in females by solitary foundresses	f'	0.75

her nephews are reproductively more valuable than her own daughters. As predicted by this hypothesis, dominants and subordinates do appear to share relatively equally in the parentage of the first workers on a nest (Field *et al.* 1998, Reeve *et al.* 2000).

Although differences in reproductive values of males and females can facilitate the invasion of pleometrosis in a haplometrotic population, such benefits are eventually lost as pleometrotic colonies become common and population sex investment ratios approach 1:1. For pleometrotic colonies to exceed 20%–30% of the population, $p_{\min}$ must be non-zero (P. Nonacs unpubl.). This upper limit can be extended when the high degree of reproductive plasticity within polistine wasps is also considered. For example, even if subordinates contribute eggs only during the part of the colony life cycle devoted to worker production, it is possible that a large percentage of these offspring will adopt reproductive strategies. These can include ascending to reproductive dominance on their natal nests, usurping weak foundresses on other nests, adopting orphaned nests, initiating their own nests immediately, or entering early hibernation and emerging the following year as foundresses (Nonacs & Reeve 1993, 1995, Gadagkar 1996, Reeve *et al.* 1998b, Starks 1998, 2001). I (unpubl. data) showed that the combination of sex ratio conflict and the production of some reproductive individuals throughout the life cycle can account for pleometrotic colonies reaching almost 50% of the population without k having to be doubled. In a similar treatment, Bourke (2001) showed that the evolution of reproductive skew in perennial multiqueen species is also affected by queen-worker conflict over sex allocation.

In summary, colony initiation in annual species of polistine wasps is an excellent study system for testing social contract models. The wasps are highly facultative in their reproductive behavior and populations are composed of liberal mixes of kin and non-kin. Cooperation between foundresses is not a function of strong nesting constraints (*see* Brockmann 1997). The animals do not defend territories larger than the immediate vicinity of the nest. Each year, offspring build new nests, and do not inherit or use their parents. Polistine wasps do not cooperatively forage, so groups do not have access to food unavailable to solitary individuals. Therefore possibly more than any other social group of animals, pleometrotic groups of wasps are reacting only to those factors within the group dynamic that directly affect reproductive success. Both observational data and manipulative experiments can reveal whether these groups form through conventions or transactions, and if the latter, how alternative reproductive options and the conditions on the nest affect skew. However, there also appear to be fundamental differences from other social groups. Transactional models may predict very different outcomes in species where groups may persist across many generations of reproductives and where ecological constraints are much more in evidence. Thus results from polistines risk being too broadly interpreted (*see* Clutton-Brock 1998, Magrath & Heinsohn 2000).

Eusocial evolution in a phenomenological context

The work of W. D. Hamilton from the 1960s and 1970s provides the foundation from which almost all current models of social behavior derive. Although his ideas revolutionized both the study of vertebrate and insect social behavior, research in both groups advanced mostly in ignorance of developments in the other. It is very encouraging that recently there have been numerous attempts at more synthetic approaches. Some authors emphasize those aspects that vertebrates and insects share in common and argue for a single evolutionary framework to explain cooperative breeding (Gadagkar 1994, Sherman *et al.* 1995). Others emphasize that clear understandings of ecological differences (Clutton-Brock 1998, Magrath & Heinsohn 2000), important evolutionary transitional states (Crespi & Yanega 1995), and phylogenetic history (Wcislo 1997) are essential for meaningful taxonomic comparisons. All of these, however, approach sociality as a taxonomic problem: i.e., to what degree is it possible to categorize species in their entirety? In contrast, the approach presented here is phenomenological in that different decisions made by an animal over its lifetime may be under differing degrees of social complexity. Thus rather than ranking a particular species as eusocial or not, I rank a particular life history decision as to whether it is made in a potentially eusocial context. If as Gadagkar (1994) and Sherman *et al.* (1995) argue that common selection pressures predominate, then one predicts vertebrates and insects in similar ecological contexts should evolve analogous solutions. If there are phylogenetic constraints, then taxon-specific solutions should predominate. Similarly, comparative studies should produce predictive models of when social contracts should be struck by convention rather than transaction.

Using a life history perspective can also facilitate the discovery of general evolutionary patterns. Clearly within eusocial species, one of the most intriguing question is the dynamics of how reproductive skew is set. Theoretical models predict that the degree of control the dominant has to set skew critically affects group structure and individual interactions (Reeve *et al.* 1998a, Johnstone 2000, Reeve & Keller 2001). Unfortunately, a dominant's degree of control may not be amenable to direct measurement (Clutton-Brock 1998, Magrath & Heinsohn 2000), and what appears as dominant con-

Table 3. Tests of transactional models and whether they are consistent with dominant control (Concession models) or joint control (Tug-of-war models) of reproductive skew. Conclusions for support with insect species are as in Reeve and Keller (2001), and with mammals, as in Clutton-Brock (1998) and Clutton-Brock *et al.* (2001). X's in both categories mean there are contradictory supportive results for both models; ?'s indicate results are consistent with both. For each species the original source is given for the results relative to reproductive skew theory. The presence of ecological or physiological differences in expected reproductive success across potential dominants and subordinates ($x_d >> x_s$) are estimated as follows from the original literature at the point where a decision to cooperate or not becomes a realistic choice. For wasps, it is whether foundresses appear to be able to succeed as solitary individuals if they chose to nest alone at the beginning of nest initiation phase. For bees, it is either at the nest initiation phase or when brood reach adulthood. For pleometrotic associations of ants, it whether being a group member greatly increases survival over being alone. For individual ant species listed, it is whether remaining in a colony as a subordinate has higher survival than dispersing to found a new colony. For mammals that are all born and raised in groups, it is at the point where subordinates reach reproductive maturity. (* Variable in that parents in some species manipulate offspring size to bias towards worker behavior.)

Species	$x_d >> x_s$	Concession	Tug-of-war
Wasps			
Polistes annularis: (Peters *et al.* 1995)	No	X	
P. bellicosus: (Field *et al.* 1998)	Yes		X
P. dominulus: (Queller *et al.* 2000, Tibbetts & Reeve 2000)	No	X	
P. fuscatus: (Reeve & Nonacs 1997, Reeve *et al.* 2000)	No	X	
Bees			
Allodapines: (Schwarz *et al.* 1998)	No*	X	
Carpenters (*Ceratina* & *Xylocopa* spp.): (Hogendoorn & Velthuis 1999)	No	X	X
Communal bees (*Andrena jacobi* & *Perdita texana*): (Paxson *et al.* 1996, Danforth *et al.* 1996)	No	X	
Halictus ligatus: (Richards *et al.* 1995, Richards & Packer 1998)	No	X	
Ants			
Pleometrosis: (Bernasconi & Strassmann 1999)	No	X	
Leptothorax spp.: (Bourke & Heinze 1994)	Yes	?	?
L. ruatus: (Rüpell, in Reeve & Keller 2001)	Yes		X
Myrmica tahoensis: (Evans 1996)	Yes		X
Mammals			
Dwarf mongoose: (Clutton-Brock 1998)	Yes	?	?
Male lions: (Clutton-Brock 1998)	Yes	?	?
Meerkat: (Clutton-Brock *et al.* 2001)	Yes		X

trol, may actually increase subordinate fitness as well (Keller & Nonacs 1993). As an alternative I propose that a more readily measurable life history character closely correlates with the control assumption. This is whether a subordinate group member has a realistic opportunity to either move to a more favorable group or to live solitarily. Even though this distinction may not be readily apparent across all species or all life stages, it is likely to be easier to determine than levels of dominant control. In essence, a realistic threat for subordinates to desert a group could force concessions from dominants. Conversely, obligate group membership would leave all individuals in a tug-of-war, irrespective of their actual ability to contest. Comparing across species, the tests of transactional models suggests that there is such a correlation (Table 3). Behavior in situations where potential subordinates have realistic options of not joining groups tends to support concession models; behavior in situations with strong constraints tends to support tug-of-war models.

The comparative life history approach also works to identify unique behaviors. For example, the phenomenon of offspring dispersing from their natal area and then joining together into cooperative groups with significant reproductive skew is almost entirely restricted to temperate polistine wasps. There are very few analogous examples in other species of similar behavior in groups of individuals of the same generation (i.e., semisocial groups: Wilson 1971). Pleometrosis as in polistines occurs in only a few tropical vespines (the sister-group to polistines), which suggests that haplometrosis was an early apomorphy in the evolution of this clade from a polistine-like ancestor (Carpenter 1991, Ross & Carpenter 1991, Spradbery 1991). Similarly, eusocial bees (Bombini, Meliponini, and Apini) are almost all haplometrotic (Ross & Carpenter 1991). In ants, pleometrosis is common during the initial stages of colony-founding, but it is a very different phenomenon from that of polistines. Either lethal fighting between females or aggression by workers almost always eliminates all but one of the original foundresses (Bernasconi & Strassmann 1999). All offspring of subordinates become workers, and die well before the colony reaches a reproductive stage. Thus in ants, pleometrosis is akin to group living or individual cooperation that facilitates rapid somatic growth rather than eusociality (Nonacs 1993). Male lions of the same generation collaborating to take over female prides is one case in vertebrates (Packer *et al*. 1991), but behaviorally-induced reproductive skew is rare in other semisocial groups. Brockmann's (1997) survey found only matrifilial groups (composed of parents and offspring) exhibit significant reproductive skew. Reeve and Keller's (1995) survey listed a number of species as having semisocial group organization, but in almost every case (except for polistine wasps), a semisocial group probable arose from a preexisting matrifilial group in which the parents had died.

In conclusion, cooperative colony initiation in temperate polistines appears inconsistent with the prediction of transactional models that reproductive non-equivalence ($x_d >> x_s$) is a prerequisite for strongly skewed reproduction. This inconsistency, however, can be explained by inclusive fitness gains gathered through a unique combination of parent-offspring conflict over sex investment ratios and plasticity in female reproductive strategies. Because few other species may share this particular combination of life history characteristics, the exception to the rule of ecological constraint may, in fact, provide even stronger evidence for the rule.

Acknowledgments

This work was supported in part by NSF grant IBN-9808788 and by funds from the Council on Research at UCLA. I thank Andrew Bourke, Smadar Gilboa, Laurent Keller and an anonymous reviewer for comments that helped me clarify and improve numerous sections of this paper. In obeisance with Hamilton's rule, Andrew Bourke and David Queller kindly provided access to unpublished manuscripts.

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