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LOWER GROUP PRODUCTIVITY UNDER KIN-SELECTED REPRODUCTIVE ALTRUISM

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Abstract.—Hamilton's rule provides the foundation for understanding the genetic evolution of social behavior, showing that altruism is favored by increased relatedness and increased productivity of altruists. But how likely is it that a new altruistic mutation will satisfy Hamilton's rule by increasing the reproductive efficiency of the group? Altruism per se does not improve efficiency, and hence we would not expect a typical altruistic mutation to increase the mean productivity of the population. We examined the conditions under which a mutation causing reproductive altruism can spread when it does not increase productivity. We considered a population divided into temporary groups of genetically similar individuals (typically family groups). We show that the spread of altruism requires a pleiotropic link between altruism and enhanced productivity in diploid organisms, but not in haplodiploid organisms such as Hymenoptera. This result provides a novel biological understanding of the barrier to the spread of reproductive altruism in diploids. In haplodiploid organisms, altruism within families that lowers productivity may spread, provided daughters sacrifice their own reproduction to raise full-sisters. We verified our results using three single-locus genetic models that explore a range of the possible reproductive costs of helping. The advantage of female-to-female altruism in haplodiploids is a well-known prediction of Hamilton's rule, but its importance in relaxing the linkage between altruism and efficiency has not been explored. We discuss the possible role of such unproductive altruism in the origins of sociality. We also note that each model predicts a large region of parameter space were polymorphism between altruism and selfishness is maintained, a pattern independent of dominance.

Key words.—Altruism, eusociality, group productivity, group selection, Hamilton's rule, kin selection, social evolution.

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The study of the evolution of altruism began with Darwin (1859). He considered in some detail the evolution of sterile female workers in insect communities and drew two important conclusions: the evolution of sterility was consistent with evolution by natural selection, provided that these workers were a net benefit to the community, and natural selection could influence the evolution of sterile individuals through selection at the family level.

It was more than 100 years before these ideas were given a theoretical framework. In his famous 1964 papers, W. D. Hamilton showed how selection through kin, soon named ''kin selection'' (Maynard Smith 1964), could favor the evolution of altruistic societies. An altruistic individual may increase its fitness indirectly by helping relatives to breed, even though this exerts a cost on its own reproduction. According to Hamilton (1964), a genetically determined altruistic trait will spread if the fitness cost (c) to the altruist (the ''helper'') is smaller than the fitness benefit (b) to the recipient of the help weighted by its coefficient of relatedness (r) with the helper:

$$br > c. \tag{1}$$

This rule is quite general given weak selection (Michod 1982; Queller 1992; Frank 1997; Roze and Rousset 2004), and it justifies Darwin's belief in family-level selection. Darwin's other proposition, that the spread of altruism occurs because of a net benefit to the community, appears to be self-evident. Indeed, the study of family-structured animal societies tends to confirm this assertion. For example, the enormous ecological success of social insects, and especially of ants, compared with other insects, demonstrates the great fitness of their cooperative kin societies at the level of populations and species (e.g., Fittkau and Klinge 1973; Hölldobler and Wilson 1990).

Hamilton (1964) defined altruism as a sacrifice of individual fitness, whereby an altruistic act results in a global loss of fitness for the altruist (i.e., a loss relative to the mean fitness of the total population), while the beneficiaries experience a global gain. Other definitions have occasionally been used (reviewed by Kerr et al. 2004), but they are not consistent with Hamilton's rule. We will follow Hamilton's view of altruism as a truly self-sacrificing behavior.

There is no doubt that enhanced group productivity promotes the spread of any trait (an effect that only disappears if productivity differences are removed by local density dependence; e.g., Taylor 1992). However, is enhanced productivity always a necessary prerequisite for the spread of altruism through kin selection? Many authors understandably assume that it is. For example, Bourke and Franks (1995, p. 84) noted that ''for altruism to evolve by kin selection, groups with altruists must be more productive than those without.'' This question is linked directly to a more general issue, the role of group productivity in the spread of traits that are individually disadvantageous but beneficial to the group, whether a family group or some other association.

The successful selection of altruism at any group level always requires that the group members are similar genetically at the locus under selection (see Nunney 2001). Thus, Hamilton's rule applies generally to traditional group selection models (e.g., Williams 1971), where the parameter r remains a measure of genetic similarity, but it does not need to be relatedness. Others have viewed group and kin selection differently, based on Wright's (1932) concept of interdemic selection (see Wade 1978, 1980). They posit that increased group productivity is both necessary and sufficient for successful group and kin selection. Here we demonstrate that, while genetic similarity within groups is a prerequisite of successful kin selection, increased productivity is not, at least in haplodiploid organisms.

It seems counterintuitive that a trait would spread despite lowering the average productivity of the groups and hence of the population. However, here we show that, while increased productivity is usually associated with the evolution of altruism through group or kin selection, this is not always the case when genetic relatedness is asymmetric. This possibility is important because it allows the evolution of productive cooperative societies in two steps: the evolution of altruistic cooperation without increased productivity, followed by the gradual refinement of the social system leading to the enhanced productivity that we associate with social groups. It is tempting to assume that reproductive altruism inevitably leads to increased productivity; however, this seems unlikely. At the very earliest stages in the shift from solitary to cooperative rearing of offspring, even a one-to-one trade-off between an offspring reared selfishly versus one reared cooperatively would be surprising, because inefficiencies resulting from the new cooperative mode of rearing offspring are likely to produce a trade-off that is less than 100% efficient. Of course, as noted above, subsequent evolution would be expected to remove this inefficiency and make cooperative breeding more productive than solitary breeding. However, in this paper we are concerned with the very earliest stages in the evolution of reproductive altruism, before such a compensatory evolution has occurred.

We focus on the asymmetric relationships among males and females under haplodiploidy, and examine the conditions when the evolution of altruism can lower group productivity. Given that haplodiploidy is the genetic system characteristic of the social Hymenoptera (bees, wasps, and ants), our result suggests that lowered productivity may be a quite general phenomenon in the early stages of social development.

CONDITIONS FOR UNPRODUCTIVE ALTRUISM: DO THEY EXIST?

To explore the effects of reproductive altruism on group productivity, we consider a family group in which there are two alternative genetically determined reproductive strategies. Either an individual reproduces normally, or it helps a close relative raise an additional b offspring, at a cost of c of its own offspring. Thus, for any $c > 0$, the helping behavior lowers an individual's reproductive success.

We assume that the optimum sex ratio in the selfish non-helping ancestral population is a Fisherian 1:1 sex ratio (Fisher 1930). The role of sex ratio is potentially very important in the evolution of social behavior (Trivers and Hare 1976), but here we will consider scenarios for the spread of altruism where we can eliminate sex-ratio effects from the interaction between altruism and productivity.

Hamilton's rule, as formulated in equation (1), shows that the trade-off between individual fitness cost (e.g., an increased risk of death) and the fitness benefit to another individual is weighted by the genetic similarity of the participants. With reproductive altruism, the cost is a decrease in the number of offspring produced by an altruistic helper (rather than any direct risk of death). Given sexual reproduction, this cost must be weighted by the relatedness of a helper to its potential offspring.

To redefine Hamilton's rule for the most general case of reproductive altruism, we need to consider the possibility that fitness costs and benefits, and relatedness may be sex dependent. We define the fitness costs to the helper of lost offspring of sex i as $c_i w_i$, the product of the number of lost offspring of sex i, weighted by their expected mating fitness, w_i (which is generally set at one for females and $(1 - a)/a$ for males, where a is sex ratio, defined as the proportion of males in the reproductive population), and likewise the benefits as $b_i w_i$. Relatedness can also be defined in a sex-dependent way so that r_{1i} is the relatedness of the helper to the relatives of sex i being raised altruistically, and r_{2i} is the relatedness between the helper and its potential progeny of sex i (male, m, or female, f). With these definitions, equation (1) becomes:

$$b_m w_m r_{1m} + b_f w_f r_{1f} > c_m w_m r_{2m} + c_f w_f r_{2f}. \qquad (2)$$

Reproductive altruism increases the productivity of the family group if:

$$b_m + b_f > c_m + c_f. \qquad (3)$$

From conditions (2) and (3) it follows that a sufficient (but not always necessary) condition for the spread of altruism without any increase in productivity is that for both sexes i:

$$1 \geq \frac{b_i}{c_i} > \frac{r_{2i}}{r_{1i}}. \qquad (4)$$

Can the condition (4) be satisfied under realistic conditions? To answer this question, we need to consider several issues.

Sexual size dimorphism can complicate the evaluation of the inequalities (3) and (4) because investment in offspring numbers may no longer be the same as investment in biomass (Trivers and Hare 1976). This distinction is not important to our discussion, and so we will assume that investment is independent of sex. In the absence of any investment bias, and given panmictic mating, the equilibrium sex ratio is 1:1 and $w_m = w_f$.

The ratio of relatedness values depends on the type of relatives being helped by the altruist. We will assume that the altruist helps raise additional offspring produced by its parents, that is, r_1 is the helper's relatedness to its full-sibs. Implicit in this assumption is that these cohesive family groups are produced by singly mated females.

We need to consider diploid and haplodiploid organisms separately. Under diploid inheritance, r_{1i} and r_{2i} are independent of sex, so that given a 1:1 population sex ratio ($w_f = w_m$), Hamilton's rule reduces to:

$$br_1 > cr_2 \qquad (5)$$

(or $bR > c$, where $R = r_1/r_2$), and equation (4) becomes the necessary and sufficient condition for the spread of unproductive altruism, with $r_{i1} = r_1$ and $r_{i2} = r_2$.

In general, condition (4) cannot be satisfied in diploid populations because $r_1 = r_2$. In the absence of inbreeding, $r_1 = r_2 = ½$, and given a regular system of inbreeding within each partially isolated colony, the genetic differences among individuals declines and relatedness increases, but the relatedness values remain equal at $(1 + 3F)/[2(1 + F)]$, where F is the inbreeding coefficient (Hamilton 1972).

In contrast, the conditions for the spread of unproductive altruism may be satisfied under a broad range of conditions given haplodiploid inheritance, the system prevailing in the majority of social insects. The necessary prerequisite is that the potential helpers are female and that they rear mainly their full-sisters. This is a general condition favoring the evolution of reproductive altruism in haplodiploid animals (Hamilton 1972). Under haplodiploidy, in the absence of inbreeding, females are related to their full-sisters by $r_{ff} = ¾$, but to their brothers by $r_{fm} = ¼$. Thus, if a hymenopteran female rears mainly full-sisters, her mean relatedness to the offspring that she helps (r_1) tends to ¾, while her relatedness to her offspring (r_2) equals ½ regardless of their sex, so that $r_1 > r_2$. If k defines her bias toward helping to raise sisters rather than brothers ($k = 0$ representing no bias; $k = 1$ defining a female that rears only her sisters), then $r_1/r_2 = R = 0.5 + k/4$.

If helping is directed efficiently to full sisters, then, as in the diploid example, Hamilton's rule for reproductive altruism (eq. 5) applies and the necessary and sufficient condition for the spread of unproductive female altruism becomes:

$$1 > \frac{b}{c} > \frac{2}{3} \tag{6}$$

(from conditions 2 and 3) because all the benefit is from raising sisters ($b_m = 0$ and $b_f = b$), and the costs are independent of sex ($c = c_f + c_m$) or result in a reduction only of daughter production ($c = c_f$).

Given some within-colony inbreeding (F), under haplodiploidy r_{2f} still equals $(1 + 3F)/2(1 + F)$, but r_{1f} is defined by:

$$r_{1f} = \frac{(3 + 5F)}{4(1 + F)} \tag{7}$$

(Hamilton 1972), so that the condition $r_1 > r_2$ still holds and the inequality (6) becomes:

$$1 > \frac{b}{c} > \frac{2(1 + 3F)}{(3 + 5F)} \tag{8a}$$

if only daughter production is sacrificed by the helper (i.e., if a helper still lays the same number of unfertilized eggs as she would if mated), or:

$$1 > \frac{b}{c} > \frac{2(1 + 2F)}{(3 + 5F)} \tag{8b}$$

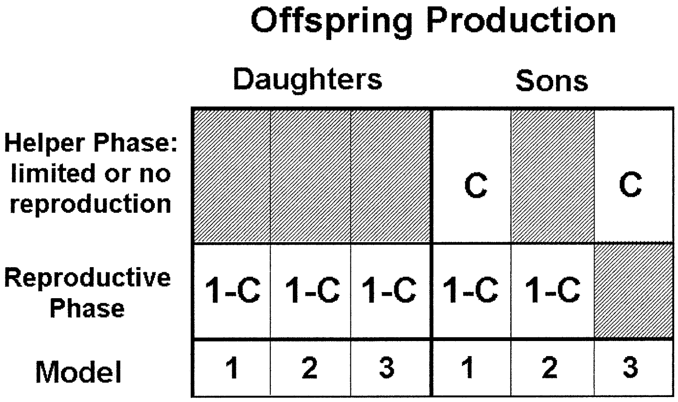
if sons and daughter production is equally affected (noting that the relatedness of a female to her haploid sons is unaffected by inbreeding, so $r_{2m} = ½$). Thus inbreeding does not qualitatively alter the conditions for the spread of unproductive altruism (although it does restrict the parameter space), and we will not consider it further.

CONDITIONS FOR UNPRODUCTIVE ALTRUISM IN HAPLODIPLOIDS: ARE THEY LIKELY IN NATURE?

The inequality (6) allows us to predict that the evolution of female worker behavior can result in lowered group productivity, provided the organism is haplodiploid and altruism is directed toward raising additional full-sib sisters. Given monogamous mating, full-sister helping requires either that helper females can discriminate the sex of the larvae or that mated females produce predominantly daughters (with unmated female productivity potentially balancing the sex ratio). Both of these possibilities are realistic in primitively social species (see Discussion). However, such generalities fail to address the crucial question of whether the parameter space consistent with the spread of unproductive altruism is large or small. To answer this question, it is necessary to develop models based on clearly defined assumptions.

To this end, we will now examine three population genetic models of a single locus segregating two alleles that determine altruistic (A) or selfish (S) behavior. Rather than using Hamilton's (1964) inclusive fitness approach to determine the change in gene frequency, we will use the ''proximity group'' method (Nunney 2001) in which an individual's fitness is evaluated conditional on the genotypes of its neighbors. In this case, the relevant neighbors of a reproductive female are her daughters. The inclusive fitness and proximity group methods are interchangeable, but the proximity group method is generally simpler when an individual is both reproductive and altruistic. We analyze the model in three ways that correspond to stages in the very early evolution of altruism. First, we examine the spectrum of altruistic alleles (based on Hamilton's rule) that could spread in the selfish population while simultaneously lowering productivity (i.e., condition 6). Second, we calculate the evolutionarily stable strategy (ESS; see Taylor and Frank 1996; Rousset 2004) that is expected to displace whatever level of altruism initially evolves, and we determine if the ESS can also lower productivity. This ESS estimation assumes weak selection, so our third approach is to consider each model in terms of strong selection, to determine if the same general conditions apply globally and, in particular, if polymorphism is a common outcome and if the altruistic ESS is resistant to invasion by selfish genotypes.

In our models, we assume that the adult life of an altruistic female is divided into two phases. Initially, she is unmated and helps raise her full-sisters. She helps for a fraction τ of her potential reproductive life, after which she mates at random with a single male and raises her own daughters for the remaining $(1 - \tau)$ of her life. Thus, the minimum cost of altruism is the loss of a fraction C $(= \tau)$ of her potential daughters. There may be additional costs depending upon how altruism influences her production of sons, because she can produce sons regardless of whether she has mated. The benefit B $(= \beta\tau)$ depends on β, the efficiency of helping, that is, the number of additional sisters produced by helping relative to the number of offspring that would have been produced selfishly.



Offspring Production	Daughters			Sons		
Helper Phase: limited or no reproduction	▨	▨	▨	C	▨	C
Reproductive Phase	1-C	1-C	1-C	1-C	1-C	▨
Model	1	2	3	1	2	3

FIG. 1. Models of sister-sister reproductive altruism under haplodiploidy. During the helper phase, unmated haplodiploid females may produce sons while they help to raise sisters. During the reproductive phase, the females produce daughters and may also produce sons. The three models differ in the effect of altruism on the production of sons. The shaded areas define zero offspring.

One important feature of these models is that the potentially important sex-ratio conflicts considered by Trivers and Hare (1976) do not arise. Each female is both a parent and a helper. As such, any sex-ratio distortions induced by the evolution of altruism can be corrected by an evolution of the intrinsic maternal sex ratio from the 1:1 ratio assumed for the ancestral population, because the panmictic mating system assumed in these models promotes a 1:1 sex ratio and avoids inbreeding.

We consider three models that differ only in the production of sons (Fig. 1). In model 1, a helping female does not mate but produces sons at a normal rate throughout her life. All altruistic costs are through a female's loss of daughters during her helping phase, prior to mating. In model 2, a helping female produces no offspring. After mating she produces the typical ratio of sons and daughters. An altruist's cost is her loss of male offspring as well as female offspring while she is a helper. In model 3, a helping female produces sons during the helping phase, but after mating she produces only daughters. As a result, helpers do not need to be able to distinguish larvae by sex. They need only to identify their mother's offspring in order to rear only sisters and sons. In this model, the cost of altruism is the early loss of daughters and the later loss of sons.

For each of the models, we can define fitnesses and recurrence relationships that predict the change in frequency of the different genotypes (Appendix 1, available online only at http://dx.doi.org/10.1554/06-115.1.s1). The fitness components of the models are defined (Table 1) and combined (Table 2) to define the productivity of each type of mating. The recurrence equations define the gene frequency change predicted by each model. In addition, we can derive an approximate condition for the spread of altruism based on Hamilton's rule and combine it with the condition for reduced productivity. The criterion for spread is complicated in a diploid or haplodiploid model by the level of dominance. To avoid this complication, we evaluate Hamilton's rule by assuming that the population is predominantly selfish and comparing the female fitness in a (rare) altruistic family (AA × A) to female fitness in a selfish (SS × S) family.

Hamilton's rule is not a rigorous condition for the invasion and fixation of altruism when fitness is nonlinear. Thus, our formulation of Hamilton's rule was compared to the two conditions of invasion: for the spread of altruism in a predominantly selfish population and for the spread of selfishness in a predominantly altruistic population (Appendix 2, available online only at http://dx.doi.org/10.1554/06-115.1.s2). Differences between these two invasion criteria indicate a region of the polymorphism, an outcome that cannot be evaluated using Hamilton's rule.

These direct comparisons between altruistic and selfish genotypes implicitly invoke strong selection. They are important because it seems very likely that a single-step mutation could switch behavior from helping to nonhelping. However, it is also plausible to expect that quantitative variation would enable weak selection to modify the time that altruistic female offspring spend helping until a local fitness maximum is reached. This maximum defines the ESS (see online Appendix 2).

Model 1: No Production of Daughters During the Helping Phase

In Model 1, a female's ability to produce sons is uninfluenced by her altruism (Fig. 1). This model defines a broad range of parameter values where reproductive altruism can spread even though it lowers family productivity. This includes all ESS strategies in which female spend less than one-third of their potential reproductive lives helping ($C <$ ⅓). The complete set of results for the case of additive altruism ($h = 0.5$ affecting both costs and benefits) are shown in Figure 2; however, the general pattern is independent of

TABLE 1. Fitness components of the single-locus haplodiploid models of altruism. The parameters are benefit ($B = \beta\tau$), cost ($C = \tau$), and dominance (h), with $B \geq 0$, $1 \geq C \geq 0$, $1 \geq h \geq 0$, where a female spends a proportion τ of her potential reproductive life helping her mother and β is the benefit of helping relative to selfish reproduction. The affect of altruism on the production of sons differs across the three models (see Fig. 1).

	Genotype		
	SS	AS	AA
Individual reproductive fitness–sons: model 1	1	1	1
model 2	1	$1 - hC$	$1 - C$
model 3	1	$1 - h + hC$	C
Individual reproductive fitness—daughters	1	$1 - hC$	$1 - C$
Maternal gain in daughter production given a brood of 100% of specified genotype	1	$1 + hB$	$1 + B$

TABLE 2. The multiplicative fitnesses defined by the three models of female reproductive altruism in haplodiploid organisms, with help directed to raising full-sisters (see Fig. 1). The table shows the progeny genotypes from each mating and the relative numbers (fitness) of each genotype produced, taking into account the cost of the prior altruism of the mother and the benefit of the current altruism of the daughters. For sons, three fitnesses are shown, corresponding to models 1, 2, and 3, respectively (see text). Parameters as in Table 1.

Maternal genotype (frequency)	Paternal genotype (frequency)			
	S(p)		A (q)	
	Daughters	Sons	Daughters	Sons
SS	SS	S	AS	S
(x)	1	1, 1, 1	$1 + hB$	1, 1, 1
AS	SS, AS	S, A	AS, AA	S, A
(y)	$(1 - hC)(1 + hB/2)$	$1, 1 - hC, hC$	$(1 - hC)[1 + (1 + h)B/2]$	$1, 1 - hC, hC$
AA	AS	A	AA	A
(z)	$(1 - C)(1 + hB)$	$1, 1 - C, C$	$(1 - C)(1 + B)$	$1, 1 - C, C$

dominance. Unproductive altruism is maintained in all of the shaded regions of the figure below the dashed line.

It is clear from Figure 2 that unproductive altruism can spread from rarity in a selfish population. This important result shows that the initial spread of altruism need not be driven by a productivity gain, and that this unproductive state can be maintained as the system evolves to its ESS. Furthermore, this productivity loss is not reversed by sex-ratio evolution occurring during and after the spread of altruism (online Appendix 1).

Model 2: No Production of Offspring during the Helping Phase

In model 2, an altruistic female produces no offspring during her helping phase (Fig. 1). The pattern of unproductive altruism is qualitatively similar to model 1 (cf. Figs. 2 and 3). The parameter space consistent with unproductive altruism is large and includes all ESS with helping at less than 20% ($C < 0.2$). Figure 3 summarizes the results given additive genetic effects ($h = 0.5$) on the benefits and costs. All ESS solutions define monomorphic altruism; however, a large proportion of parameter space defines polymorphism.

Model 3: No Production of Daughters during the Helping Phase and No Production of Sons during the Reproductive Phase

In model 3, an altruistic female produces sons during the period that she is unmated and helping to raise her sisters, but after she mates and begins independently reproducing, she produces only daughters (Fig. 1). Thus, in this model the costs of altruism are distributed throughout the female's adult life: the loss of daughters during the helping period, C, and the loss of sons during the reproductive period, $1 - C$. Under model 3, as in models 1 and 2, reproductive altruism can invade a selfish population and lower productivity. However, model 3 altruism cannot spread to fixation (under plausible conditions) regardless of its effect on productivity. Also unlike the previous models, the pattern of global behavior predicted under strong selection is qualitatively different from

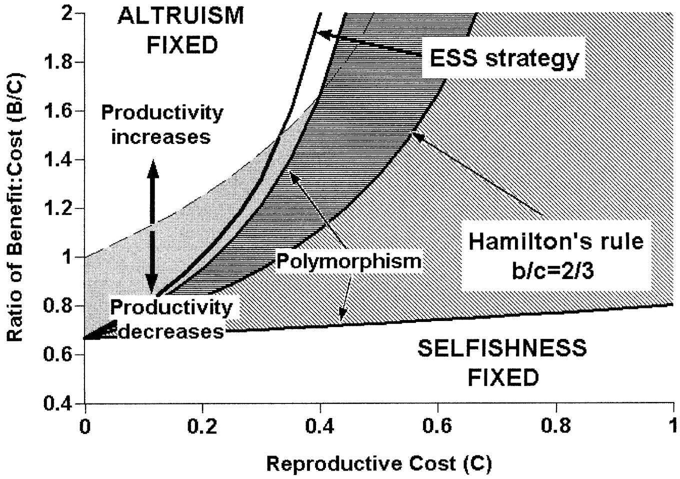


FIG. 2. The evolution of reproductive altruism in haplodiploid organisms in the single-locus multiplicative model 1 (see Fig. 1). The results are shown as a function of the cost ($C = \tau$, the proportion of time spent helping) and the benefit (B) -to-cost ratio ($= \beta$, the efficiency of helping). Gray region: altruism fixed, but population productivity reduced by altruism. Shading: region of polymorphism and productivity reduced, with altruism predominating above the line defining Hamilton's rule ($b/c = ⅔$; see condition 6). The curve defining the evolutionarily stable strategy is never within the polymorphic region. In this example, the altruism is additive for cost and benefit ($h = 0.5$; see text).

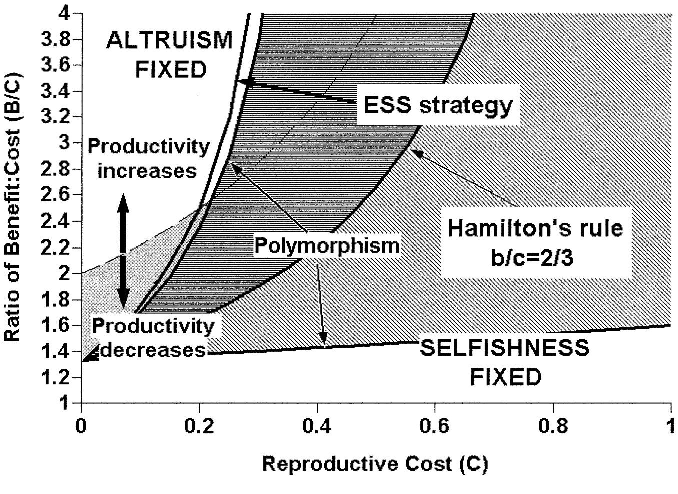


FIG. 3. The evolution of reproductive altruism in haplodiploid organisms in the single-locus multiplicative model 2 (see Fig. 1). The results are shown as a function of C, the proportion of time spent helping, and B/C, the efficiency of helping. For further details, see Figure 2.

the predictions of the ESS analysis. For example, ESS parameter combinations occur within the region where altruism cannot spread. This occurs because the selfish and altruistic strategies are qualitatively different, so that an altruistic fitness maximum does not guarantee superiority to selfish genotypes.

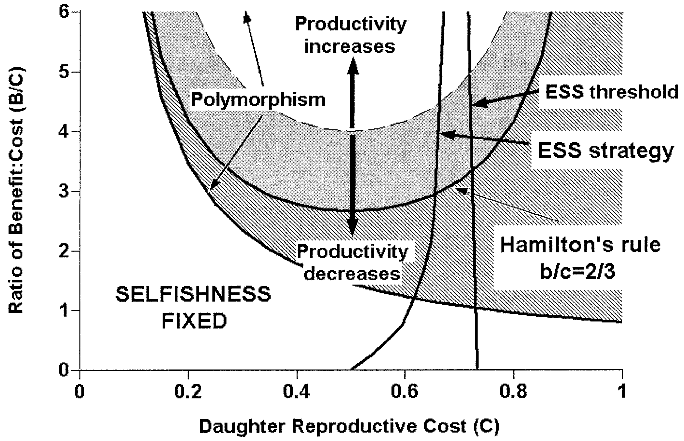


FIG. 4. The evolution of reproductive altruism in haplodiploid organisms in the single-locus multiplicative model 3 (see Fig. 1). The results are shown as a function of *C*, the proportion of time spent helping (and when helpers produce sons) and *B*/*C*, the efficiency of helping. For further details, see Figure 2. The vertical line labeled ''ESS threshold'' defines the point beyond which the evolutionarily stable strategy disappears.

DISCUSSION

In the past, it has been widely assumed that the spread of altruism requires an increase in group productivity (e.g., Wade 1980; Bourke and Franks 1995). We have shown that under diploidy, this pleiotropic link between altruism and increased productivity is generally necessary, but that under haplodiploidy, the evolution of reproductive altruism does not need to be associated with increased group productivity. This difference is important because there is no a priori reason why an altruistic mutation should also increase group productivity. Indeed, the distribution of reproductive altruism in nature is consistent with the view that pleiotropy between reproductive altruism and increased productivity is unusual and arises predominantly when there are strong ecological constraints against dispersal and outbreeding. Theoretical and empirical studies indicate that the intensity of the reproductive skew shown by an animal society (i.e., the uneven sharing of reproduction among its members) increases with the constraints against dispersal (Emlen 1991, 1997; Jarvis et al. 1994; Keller and Reeve 1994; Bourke 1997; Thorne 1997; Faulkes and Bennett 2001). Extreme reproductive altruism (i.e., sexual abstinence of most individuals) in diploid animals is rare and associated with harsh living conditions that make colonization difficult and lead to local inbreeding (Reilley 1987; Reeve et al. 1990; O'Riain 1996; Thorne 1997; Braude 2000; Cooney and Bennett 2000; Faulkes and Bennett 2001). In contrast, severe constraints against dispersal and outbreeding are not typical prerequisites for the evolution of helping in haplodiploids. This suggests that helping becomes the more productive option for most individuals when dispersing, outbreeding, and founding of new family units is impaired by harsh environmental conditions, and that this is generally a necessary prerequisite for helping to evolve in diploids. However, increased productivity is not a necessary prerequisite in haplodiploid species, and it is in these species that reproductive altruism has repeatedly evolved (Brockmann 1984), without high levels of inbreeding (Werren 1993).

Altruism can spread in haplodiploids even when it results in a drop in productivity because full-sisters are more related to each other than they are to their potential offspring. We analyzed three models of reproductive altruism in which altruistic females sacrificed part of their reproductive potential to help their mother by raising additional sisters. After the helping phase, the altruistic females mated and began reproducing independently. The three models differed in the nature of the reproductive cost of helping. However, in each model a broad range of conditions exists where the evolution of helping is favored even though group (family) productivity decreased (Figs. 2–4).

While increased productivity is not a necessary feature of kin selection, it is certainly true that the link between evolutionary success and increased productivity predominates under all forms of selection, including individual selection. The link is typically observed because, in general, the number of gene copies passed on (measuring fitness) is equal to or less than the number of individuals produced (measuring productivity). In a diploid sexual system, fitness and productivity correspond between parent and offspring because each parent passes one gene copy to each offspring. In the case of sisters raising sisters in haplodiploid organisms, each sister successfully raised represents one individual, but also represents 1.5 gene copies. For this reason, the spread of sister-sister altruism in haplodiploid organisms, through the spread of ''altruistic'' alleles, is not directly linked to an increase in productivity.

The essential prerequisite for the evolution of altruistic traits within any kind of group structure, regardless of the details of inheritance, is not enhanced group productivity but the nonrandom association and interaction of similar genotypes. More precisely, traditional group selection (including kin selection) can be defined as that component of natural selection due to the positive association of similar genotypes (Nunney 1985). Under this definition, it becomes clear that Hamilton's rule applies generally, with kin selection as the important special case where the positive association is due to the interaction of close family members. Other positive associations may drive different forms of group selection (e.g., the green-beard effect, Dawkins 1976; the maintenance of sex, Nunney 1989, 1999).

We used Hamilton's rule to define the conditions expected to favor the spread of reproductive altruism. We demonstrated the accuracy of Hamilton's rule in models 1 and 2 (Figs. 2, 3), even though the derivation of the rule is based on several restrictive assumptions (see Michod 1982) violated by our including strong selection in our multiplicative models. Even so, Hamilton's rule was a good indicator of whether the altruistic phenotype would spread to a frequency of more than 0.5; however, as the cost (*C*) increased, the parameter space leading to a stable polymorphism increased (see Figs. 2–4). Thus, as C increased, the rule became too restrictive in predicting whether altruism could spread from rarity and not restrictive enough in predicting whether altruism could exclude selfishness. Model 3 provided an interesting case because selfish behavior was qualitatively different from altruistic behavior. As a result, strong selection (i.e., allelic changes shifting from altruism to selfishness) gave results consistent with Hamilton's rule, while a weak selection ESS approach did not.

In models 1 and 2, the ESS value of C predicted from a given value of B/C ($= \beta$, the efficiency of the altruism) always defined monomorphic altruism, but the ESS did not necessarily increase productivity. Thus, even after the initial spread of altruism, the more subtle secondary evolution to the ESS does not change the general conclusion: altruism can spread despite lowering productivity. Of course, productivity is expected to increase over the longer term as the value of β increases, that is, as the efficiency of the altruistic helping improves. Varying the level of dominance in these models had no significant effect on the outcome (but see Roze and Rousset 2004).

More than 20,000 species of Hymenoptera are social: all the ants and many species of bees and wasps. They live in small associations of reproductive females and their dependent offspring (called subsocial or semisocial colonies, depending on the relatedness between the reproductive females) or in numerous and often complexly organized societies called eusocieties. These latter are formed by one or a few reproductive (singly or multiply mated) females, their young progeny, and their numerous sterile adult daughters that work together to feed and defend the entire society (Wilson 1971; Lin and Michener 1972). While most or all authors recognize the determinant role of kin selection in the evolution of hymenopteran societies, the specific role of haplodiploidy in this evolution is still being discussed (Bourke and Franks 1995). Theoretically, haplodiploidy favors the evolution of reproductive altruism in females (in the form of rearing full-sisters) if two conditions are satisfied: (1) rearing full-sisters must increase female fitness more than rearing brothers; and (2) the females must have the opportunity to raise mostly full-sisters.

Let us consider the first condition. The benefit to the helper of rearing a full-sister depends not only on their relatedness, but also on the relative fitness of the females, which varies inversely with their ratio in the population (Trivers and Hare 1976). In primitively social populations where the global sex ratio is 1:1, full-sister helping is advantageous. In the three models of primitive sociality that we examined, the evolution of altruism alters the sex ratio but over the longer term natural selection favors a return to a 1:1 sex ratio. We have shown that when unproductive altruism spreads, it remains unproductive as the population returns to a 1:1 sex ratio.

Our three models retain a 1:1 sex ratio because they preclude worker control of the sex ratio: the workers never rear their male siblings; instead, all male offspring are reared (i.e., provisioned) by their mother. Trivers and Hare (1976) pointed out that if workers can preferentially rear female over male siblings, then the sex ratio of the population progressively increases toward an equilibrium value of 3:1 (female: male). At that point, a worker gains the same benefit from rearing a sister or a brother. This is a possibility that becomes more likely as a division of labor in the colony becomes more extreme.

The second (and potentially more problematic) condition of preferential rearing of full-sisters presupposes monogamy (or an ability of helpers to discriminate the genetic relatedness of the brood) and either that some or all of the broods produced by singly mated females are female biased (or that helpers are able to discriminate between the sexes and against males). These prerequisites are found in some eusocial and primitively social species of Hymenoptera. Many primitively social as well as eusocial hymenopteran species are obligatorily or facultatively monogamous (see Hölldobler and Wilson 1990; Seger 1991), and many of them show spatially or temporally skewed sex ratios, with female bias (and mostly female raising) associated with the presence of a single monogamous foundress in the colony, and male bias (with mostly male raising) associated either with the absence of the foundress (Yanega 1989; Mueller 1991; Bourke 1994), the presence of a multimated queen (Bourke and Chan 1994; Sundström 1994; Passera and Aron 1996), or the presence of several queens (Evans 1995).

In evolved eusocial species, workers commonly discriminate the sex of the eggs or larvae and are able to assess either the maternal origin and the mean relatedness asymmetry of the brood in their colony (although not to discriminate among patrilines; Carlin 1988; Keller 1995). This enables them to kill less-related males—or even ''misbehaving'' male-producing queens—and raise more-related kin (Ratnieks and Visscher 1989; Bourke 1994; Passera and Aron 1996), which can mean raising more full-sisters (Evans 1995; Sundström et al. 1996). Primitively social hymenopteran are assumed to behave more simply. They are generally assumed to be unable to distinguish between sexes in the brood but able to discriminate eggs by their maternal origin, and they have commonly been observed eating the eggs laid by other nestmates or workers in the nest (Brothers and Michener 1974; Velthuis 1977; West-Eberhard 1978). Sex discrimination within a brood has not yet been demonstrated in the primitively social Hymenoptera, but it has not been excluded. In any case, sex discrimination is not a required condition for raising mostly full-sisters.

In nature, the mechanism of split sex ratio allows mostly full-sister raising without sex discrimination by female helpers, while the global sex ratio stays below 3:1 and possibly around 1:1. A population has a split sex ratio when it contains two spatial or temporal kinds of groups showing different but predictable sex ratios (Grafen 1986). Split sex ratios involving full-sister raising in (at least temporarily) female-skewed colonies have been observed or experimentally verified in some primitively social wasps and bees (Jeanne 1980; Seger 1983; Yanega 1989; Boomsma and Grafen 1990; Mueller 1991).

It has been proposed that such split ratios can satisfy the prerequisites for the evolution of full-sister helping in primitively social Hymenoptera provided female-skewed colonies are typically founded by a single monogamously mated foundress (Werren and Charnov 1978; Seger 1983; Grafen 1986; Stublefield and Charnov 1986; Godfray and Grafen 1988).

Under these conditions, most females are born in female-skewed colonies or become adults and possibly helpers when their mother lays mostly female eggs (Seger 1983, 1991). Consequently, helping is mostly directed toward full-sisters, and males may be raised predominantly by their mothers. This being the case, split ratios will also satisfy the conditions for the evolution of unproductive altruism.

Even at this stage of primitive cooperation, an evolutionary conflict about the production of male eggs arises between the two generations of adult females sharing the same nest. Selection will favor agonistic or parasitic behaviors allowing the foundress to replace the eggs laid by other females in the group with her own (Trivers and Hare 1976; Charnov 1978). Such behaviors are indeed common traits of primitive hymenopteran societies (Michener and Brothers 1974; Brockman 1984). Thus, the evolution of helping in primitive hymenopteran societies may be enforced by maternal dominance or parasitism. In this case, one can expect that the aggressive and cannibalistic behavior of the foundresses reduces the overall productivity of the groups, that is, leads to unproductive altruism.

This link of dominant behaviors to altruism illustrates two important points. First, the steps promoting reproductive altruism are unlikely to enhance productivity: in this example, full-sister raising due to maternal parasitism has at a minimum a slight cost (the helper eggs replaced by a mother's egg), which must lead to unproductive altruism. Second, helping behavior may be either active or passive. In other words, an altruistic daughter in a female-skewed colony may either actively restrain her egg laying and directly care for her mother's (mostly female) brood, or, in the passive case, lay eggs at the usual rate but let her mother replace some of them. The replacement eggs are more valuable because they are mostly full-sisters. These two possibilities are almost equivalent in terms of evolutionary genetics, with the slight difference of the energetic loss due to the production of some eggs doomed to feed the mother. Note that acceptance of maternal parasitism by daughters is evolutionarily favored in female-skewed societies founded by one singly mated foundress, but only approaches neutrality in societies with a balanced 1:1 sex ratio (Charnov 1978).

Sociality and eusociality have evolved numerous times in Hymenoptera (Snelling 1981), presumably originating with the spread of relatively simple helping behavior (Lin and Michener 1972; West-Eberhard 1978). Altruistic cooperation that enhances productivity needs to be well organized (Hölldobler and Wilson 1990), because either resources must be used more efficiently or more resources must be gathered. But how does such organization evolve in a single step from the ancestral selfish behavior? While most evolved eusocieties are very productive, due to their high organization, primitive societies are far less organized and less productive (e.g., Wilson 1971).

The development of efficient (i.e., productive) organization of cooperative groups is complicated by the many evolutionary conflicts that exist between their members. Due to their genetic structure, the sources of conflicts are numerous in haplodiploid societies (Trivers and Hare 1976; Fisher and Pomeroy 1990; Seger 1991; Bourke 1997). Although these conflicts can be efficiently resolved in evolved eusocieties (e.g., Ratnieks and Visscher 1989), they may be costly in primitive (poorly organized) societies. Indeed, aggression between members is frequently observed in primitive hymenopteran societies (Velthuis 1977; West-Eberhard 1978; Seger 1991; Bourke 1997).

A high level of intragroup aggression is likely to significantly reduce the productivity of the group. However, as we have shown here, unproductive altruism can evolve provided that it increases the inclusive fitness of the helper genotype. These findings suggest that the highly productive eusocieties of ants and bees may have originated with an initial step of unproductive altruism.

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Literature Cited

Boomsma, J. J., and A. Grafen. 1990. Intraspecific variation in ant sex ratios and the Trivers-Hare hypothesis. Evolution 44: 1026–1034.

Bourke, A. F. G. 1994. Worker matricide in social bees and wasps. J. Theor. Biol. 167:283–292.

———. 1997. Sociality and kin selection in insects. Pp. 203–227 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 4th ed. Blackwell, London.

Bourke, A. F. G., and G. L. Chan. 1994. Split sex ratios in ants with multiple matings. Trends Ecol. Evol. 9:120–122.

Bourke, A. F. G., and N. R. Franks. 1995. Social evolution in ants. Princeton Univ. Press, Princeton, NJ.

Braude, S. 2000. Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. Behav. Ecol. 11:7–12.

Brockmann, H. J. 1984. The evolution of social behaviour in insects. Pp. 340–361 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 2nd ed. Blackwell, Oxford, U.K.

Brothers, D. J., and C. D. Michener. 1974. Interactions in colonies of primitively social bees. III. Ethometry of division of labor in *Lasioglossium zephyrum*. J. Comp. Physiol. 90:129–168.

Carlin, N. F. 1988. Species, kin and other forms of recognition in the brood discrimination behavior of ants. Pp. 267–295 *in* J. C. Trager, ed. Advanced in myrmecology. Brill, Leiden.

Charnov, E. L. 1978. Evolution of eusocial behavior: Offspring choice or parental parasitism? J. Theor. Biol. 75:451–465.

Cooney, R., and N. C. Bennett. 2000. Inbreeding avoidance and reproductive skew in a cooperative mammal. Proc. R. Soc. Lond. B 267:801–806.

Darwin, C. 1859. On the origin of species by means of natural selection or the preservation of favored races in the struggle for life. Murray, London.

Dawkins, R. C. 1976. The selfish gene. Oxford Univ. Press, Oxford, U.K.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. Pp. 301–337 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 3rd ed. Blackwell, Oxford, U.K.

———. 1997. Predicting family dynamics in social vertebrates. Pp. 305–339 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 4th edition. Blackwell Oxford, U.K.

Evans, J. D. 1995. Relatedness threshold for the production of female sexuals in colonies of a polygynous ant, *Myrmica tahoensis*, as revealed by microsatellite analysis. Proc. Natl. Acad. USA 92:6514–6517.

Faulkes, C. G., and N. C. Bennett. 2001. Family values: group dynamics and social control of reproduction in African mole-rats. Trends Ecol. Evol. 16:184–190.

Fischer, R. M., and N. Pomeroy. 1990. Sex-discrimination and infanticide by queens of the bumble bee *Bombus terrestris* (Hymenoptera, Apidae). Anim. Behav. 39:801–802.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford Univ. Press, Oxford, U.K.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica 5: 2–14.

Frank, S. A. 1997. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51: 1712–1729.

Godfray, H. C. J., and A. Grafen. 1988. Unmatedness and the evolution of eusociality. Am. Nat. 131:303–305.

Grafen, A. 1986. Split sex ratios and the evolutionary origins of eusociality. J. Theor. Biol. 122:95–121.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I and II. J. Theor. Biol. 7:1–52.

———. 1972. Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. 3:193–232.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard Univ. Press, Cambridge, MA.

Jarvis, J. U. M., M. J. O'Riain, N. C. Bennett, and P. W. Sherman. 1994. Mammalian eusociality: a family affair. Trends Ecol. Evol. 9:47–51.

Jeanne, R. L. 1980. The evolution of social behaviour in the Vespidae. Annu. Rev. Entomol. 25:317–396.

Keller, L. 1995. Social life: the paradox of multiple-queen colonies. Trends Ecol. Evol. 10:355–360.

Keller, L., and H. K. Reeve. 1994. Partitioning of reproduction in animal societies. Trends Ecol. Evol. 9:98–103.

Kerr, B., P. Godfrey-Smith, and M. W. Feldman. 2004. What is altruism? Trends Ecol. Evol. 19:135–140.

Lin, N., and C. D. Michener. 1972. Evolution of sociality in insects. Q. Rev. Biol. 47:131–159.

Maynard Smith, J. 1964. Group selection and kin selection. Nature 201:1145–1147.

Michener, C. D., and D. J. Brothers. 1974. Were workers of eusocial hymenopteran initially altruistic or oppressed? Proc. Natl. Acad. Sci. USA 71:671–674.

Michod, R. E. 1982. The theory of kin selection. Annu. Rev. Ecol. Syst. 13:23–55.

Mueller, U. G. 1991. Haplodiploidy and the evolution of facultative sex ratios in a primitively eusocial bee. Science 254:242–244.

Nunney, L. 1985. Group selection, altruism, and structure-deme models. Am. Nat. 26:212–230.

———. 1989. The maintenance of sex by group selection. Evolution 43:245–257.

———. 1999. Lineage selection: natural selection for long-term benefit. Pp. 238–252 *in* L. Keller, ed. Levels of selection in evolution. Princeton Univ. Press, Princeton, NJ.

———. 2001. Population structure. Pp. 70–83 *in* C. R. Fox, D. Roff, and D. Fairbairn, eds. Evolutionary ecology: concepts and case studies. Cambridge Univ. Press, Cambridge, U.K.

O'Riain, M. J., J. U. M. Jarvis, and C. G. Faulkes. 1996. A dispersive morph in the naked mole-rat. Nature 380:619–621.

Passera, L., and S. Aron. 1996. Early sex discrimination and male brood elimination by workers of the Argentine ant. Proc. R. Soc. Lond. B 263:1041–1046.

Queller, D. C. 1992. A general model for kin selection. Evolution 46:376–380.

Ratnieks, F. L. W., and P. K. Visscher. 1989. Worker policing in the honeybee. Nature 342:796–797.

Reeve, H. D., D. F. Westneat, W. A. Noon, and P. W. Sherman. 1990. DNA ''fingerprinting'' reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proc. Natl. Acad. Sci. USA 87:2496–2500.

Reilley, L. M. 1987. Measurements of inbreeding and average relatedness in a termite population. Am. Nat. 130:339–349.

Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton Univ. Press, Princeton, NJ.

Roze, D., and F. Rousset. 2004. The robustness of Hamilton's rule with inbreeding and dominance: kin selection and fixation probabilities under partial sib mating. Am. Nat. 164:214–231.

Seger, J. 1983. Partial bivoltinism may cause sex-ratio biases that favour eusociality. Nature 301:59–62.

———. 1991. Cooperation and conflict in social insects. Pp. 338–373 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 3rd ed. Blackwell, London.

Snelling, R. R. 1981. Systematics of social Hymenoptera. Pp. 369–453 *in* H. R. Hermann, ed. Social insects, Vol. 2. Academic Press, London.

Stubblefield, J. W., and E. L. Charnov. 1986. Some conceptual issues in the origin of eusociality. Heredity 57:181–187.

Sundström, L. 1994. Sex ratio bias, relatedness asymetry and queen mating frequency in ants. Nature 367:257–258.

Sundström, L., M. Chapuisat, and L. Keller. 1996. Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. Science 274:9993–9995.

Taylor, P. D. 1992. Inclusive fitness in a homogeneous environment. Proc. R. Soc. Lond. B 249:299–302.

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. J. Theor. Biol. 180:27–37.

Thorne, B. L. 1997. Evolution of eusociality in termites. Annu. Rev. Ecol. Syst. 28:27–54.

Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of the social insects. Science 191:249–263.

Uyenoyama, M. K., and M. W. Feldman. 1982. Population genetic theory of kin selection. II. The multiplicative model. Am. Nat. 120:614–627.

Velthuis, H. H. W. 1977. Egg laying, aggression and dominance in bees. Pp. 436–449 *in* Proceedings of the 15th international congress on entomology. August 19–27, 1976, Washington, DC. Entomological Society of American, College Park, MD.

Wade, M. J. 1978. A critical review of the models of group selection. Q. Rev. Biol. 53:101–114.

———. 1980. Kin selection: its components. Science 210:665–667.

Werren, J. H. 1993. The evolution of inbreeding in haplodiploid organisms. Pp. 42–59 *in* N. Wilmsen Thornhill, ed. Natural history of inbreeding and outbreeding. Univ. Chicago Press, Chicago.

Werren, J. H., and E. L. Charnov. 1978. Facultative sex ratios in wasps and bees. Nature 272:349–350.

West-Eberhard, M. J. 1978. Polygyny and the evolution of social behaviour in wasps. J. Kans. Entomol. Soc. 51:832–856.

Wilson, E. O. 1971. The insect societies. Harvard Univ. Press, Cambridge, MA.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. VI Intern. Congr. Genet. 1: 356–366.

Yanega, D. 1989. Caste determination and differential diapause within the first brood of *Halictus rubicundus* in New York. Behav. Ecol. Sociobiol. 24:97–107.

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