ing her young, whereas in others, helpers are unlikely to breed with the dominant female, and either kin selection or mutualism probably maintains cooperation (*5*). Similarly, the available evidence suggests that the relative importance of mutualism and kin selection may vary between societies.

Finally, if mutualism proves to be important in maintaining cooperative animal societies, the benefits of cooperation in animals may be more similar to those of cooperation in humans than has been previously supposed. In humans, unrelated individuals commonly assist each other (*59*), generalized reciprocity appears to be important in maintaining many social institutions (*60*), and, where human groups compete, their size often has an important effect on the outcome (*61*). "God," as Shaw's cynical Bastard of Orléans remarks to an optimistic Joan of Arc, "is on the side of the big battalions." All three trends appear to have close parallels in other cooperative animals.

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62. I thank J. Strassmann, A. Russell, P. Brotherton, R. Johnstone, H. Kokko, A. Cockburn, C. Packer, A. Young, and S. West for their generous comments on previous drafts, and A. Carlson for her help.

REVIEW: CONFLICT AND COOPERATION

Cooperation and Competition Between Relatives

Stuart A. West,* Ido Pen,† Ashleigh S. Griffin

Individuals are predicted to behave more altruistically and less competitively toward their relatives, because they share a relatively high proportion of their genes (e.g., one-half for siblings and one-eighth for cousins). Consequently, by helping a relative reproduce, an individual passes its genes to the next generation, increasing their Darwinian fitness. This idea, termed kin selection, has been applied to a wide range of phenomena in systems ranging from replicating molecules to humans. Nevertheless, competition between relatives can reduce, and even totally negate, the kin-selected benefits of altruism toward relatives. Recent theoretical work has clarified the processes and selective forces underlying this effect and has demonstrated the generality of the effect of competition between relatives.

Kin selection theory provides a solution to the problem of altruism (*1*, *2*). The problem is, why should an individual forego reproduction, and instead help another to breed (e.g., in cooperatively breeding birds, in mammals such as meerkats, or in social insects such as ants, bees, wasps, and termites)? This can be explained relatively easily if they are helping their close relatives reproduce and hence are still passing on their genes to the next generation, albeit indirectly. A pleasingly simple and elegant way of quantifying this idea of kin selection is Hamilton's rule (*1*, *2*). This states that individuals will be selected to perform altruistic behaviors for the benefit of relatives when $rb - c > 0$, where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary, and r is their genetic relatedness.

More generally, kin selection theory and Hamilton's rule can be applied to any situation involving conflict or cooperation. For example, it has been suggested that in birds and mammals, individuals are more likely to warn close relatives about the approach of predators; or that higher relatedness between parasites within a host will lead to less intense competition for the host resources, and so lower damage (virulence) to the host (*1–4*). Furthermore, kin selection theory is fundamental to explaining conflicts of interest between relatives. For example, an individual passes on one-half of its genes to her own offspring, but on average shares only one-fourth of her genes with those in the offspring of a brother or sister (full sibling), and so an individual should value her own reproduction twice as much as her brother's or sister's. Consideration of such conflicts of interest have been particularly successful in explaining the social behavior of social insects, where reproductive interests of the queens and their workers can often differ (*5*, *6*).

Here, we are concerned with the often-neglected fact that altruistic behavior toward relatives may at some later time lead to increased competition between relatives, reducing or even completely removing the net selective advantage of altruism (*4*, *7–16*). Put simply, altruism toward a relative is less advantageous if their increased fitness comes at a cost to your other relatives.

Does Limited Dispersal Favor Altruism?

Hamilton suggested that limited dispersal of individuals from the natal group (population viscosity) would increase the relatedness between interacting individuals, and so would be an important factor favoring altruism (*2*, *3*, *17*, *18*). This idea has since been applied widely. For example, it has been argued that limited dispersal favors (i) cooperative breeding and helping in birds, mammals and insects; (ii) lower levels of aggression between male insects competing for mates; (iii) lower virulence in parasites such as malaria; (iv) female-biased sex ratios in insects; and (v) supposedly altruistic traits in bacteria such as nitrogen fixing in *Rhizobium* that infect legumes (*2*, *3*, *17–23*).

There is a problem with this idea, however. Although limited dispersal may favor altruism because it increases relatedness between potential altruists and their beneficiaries, it may also increase relatedness between potential competitors, which opposes altruism (*17*, *18*). Clearly, the fundamental question is, what is the net effect of these two opposing forces? A number of "limited-dispersal" models have been developed to address this question. For example, Taylor (*11*) considered an "island model" in which the population is made up of discrete groups (patches). Each patch contains N females, who interact (may be altruistic to each other), breed, and then die. The offspring mate at random on each patch and then, with some probability t, disperse to distant patches, after which competition occurs for the N breeding sites. Taylor found the simple and rather surprising result that the benefits of increased relatedness that arise as a result of limited dispersal are exactly canceled by the cost of increased competition between relatives. Consequently, the dispersal rate t has no overall effect on selection for altruism. The same result has been found with a number of approaches, including when other types of population structure are considered, such as stepping-stone models where individuals are located on a grid and disperse locally (*9*, *10*, *13*, *15*).

Crucially, these models assume that population regulation is locally inelastic (*10*)—the population density per patch is fixed by external factors. Assuming that patch productivity increases with the number of altruists in it, offspring born in patches that contain more altruists will suffer greater reproductive competition (local competition or soft selection). This greater competition between relatives negates the advantage of increased relatedness on the patch. However, limited dispersal can favor altruism when patches containing more altruists do better. Ways in which this can happen include (i) altruism occurs (between offspring) before dispersal, and competition occurs after dispersal (*11*, *13*, *24*); (ii) the capacity of the environment expands, allowing more altruistic patches to have a higher population density (elastic or hard selection) (*4*, *10*, *11*, *15*, *16*, *25*); (iii) overlapping generations increases relatedness between altruists and beneficiaries, but not the probability that relatives will compete (*12*); and (iv) density dependence occurs with a time lag between generations (*26*). The crucial point about all these possibilities is that relatedness is increased locally at the point when altruism may occur (favoring altruism), but that competition occurs more globally among the whole population (reducing competition between relatives).

Overall, the models show that a lower level of dispersal can favor altruism because it increases relatedness, but that this can be canceled by the increased competition between relatives that can also result from limited dispersal. In models in which one sex disperses more than the other, altruism can be more than totally canceled, and individuals can be selected to be spiteful to their neighbors (*10*, *13*). Consequently, when limited dispersal is observed to lead to close relatives interacting, it should not be assumed to mean that kin selection will be a strong force favoring altruistic behaviors. The extent to which competition between relatives is important in a specific example will depend upon the details of natural history, especially the pattern of dispersal and the scale at which competition occurs (local or global).

Applying Hamilton's Rule Correctly

The influence of competition between relatives on kin selection can be explored with properly enhanced versions of Hamilton's rule (*4*, *7*, *14*). The first step is to extend Hamilton's rule (*28*) to include all individuals whose fitness is affected by a behavior, which gives:

$$r_{xy}b - c - r_{xe}d > 0 \qquad (1)$$

where r_{xy} is the altruist's relatedness to the beneficiary of its altruism (i.e., the standard r), r_{xe} is the altruist's relatedness to the individuals who suffer the increased competition from the beneficiary (and possibly reduced competition from the altruist), and d is the general decrement in fitness associated with the altruistic act (*7*). If the altruist is unrelated to the competitors of the beneficiary ($r_{xe} = 0$) or the altruistic act leads to no increase in the general level of competition ($d = 0$), then the classic equation for Hamilton's rule holds. As the altruist becomes more related to the competitors of the beneficiary (increasing r_{xe}, as, for example, when competition becomes more local) and/or the altruistic act increases the general level of competition (increasing d), the kin selection advantage in being altruistic is reduced. In the extreme, with inelastic population regulation ($b = c + d$), if an individual is equally related to the beneficiary of their altruism and their competitors ($r_{xy} = r_{xe}$), then altruism cannot be favored, irrespective of the values of b and c.

How can competition between relatives be allowed for in empirical studies of kin selection? The ideal solution to this problem would be to measure all of the parameters in Eq. 1. Unfortunately, this could be extremely difficult. In the next sections we describe some methodologies that allow competition between relatives to be incorporated into empirical studies (via Hamilton's rule) more easily. These methodologies are based on the simplifying assumption that the increased reproductive success of the beneficiary is exactly matched by a decrease in reproductive success of others (i.e., $b = c + d$). This can often be a reasonable approximation because no population can expand indefinitely (*10*, *14*). However, these methodologies would overestimate the importance of competition between relatives in populations where $b > c + d$.

Competition and r

Queller (*14*) provided a methodology for incorporating competition between relatives

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Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, UK.

*To whom correspondence should be addressed. E-mail: stu.west@ed.ac.uk.

†Present address: Theoretical Biology, Center for Ecological and Evolutionary Studies, University of Groningen, NL-9751NN Haren, Netherlands.

into the r term of Hamilton's rule. To proceed further, we must define relatedness more precisely. In particular, it is important to remember that relatedness coefficients measure genetic similarity relative to the population mean. A general definition of the relatedness coefficient (r) has been provided by Grafen (*29*), who showed that, considering an altruistic allele, relatedness $r = \Sigma(p_y - \bar{p})/\Sigma(p_x - \bar{p})$, where $\bar{p}$ is the population frequency of the altruist allele, p_x is the frequency of the allele in all performers of altruism, and p_y is the frequency of the allele in the beneficiaries of altruism. Methods for measuring relatedness on the basis of this definition make use of data from a number of neutral molecular markers, such as microsatellites, and essentially measure pedigree (*27*). The importance of the scale at which r is estimated (i.e., the base population) can be illustrated by considering the relatedness between two brothers (full siblings). If we measure their relatedness with respect to a large outbreeding population, then we would obtain the expected $r = 0.5$. However, at the other extreme, if we measure it with respect to only other brothers, then the frequency of the altruism allele (or molecular markers used) will be, on average, the same for all the brothers ($p_y = \bar{p}$), and so $r = 0$. The point here is that relatedness is a statistical concept; so, when two individuals are close relatives, they do not necessarily have a high relatedness (*14*).

Queller (*14*) showed that Hamilton's rule, $rb - c > 0$, is equivalent to Eq. 1, as long as relatedness is measured at the correct scale—specifically, if relatedness to the beneficiary of altruism (r) is measured with respect to the individuals with which the beneficiary will compete (defined here as r_c), rather than with respect to the global population (r_{xy}). This result is particularly useful because it illustrates clearly how the consequences of competition between relatives may have been ignored in empirical studies. In organisms such as cooperative breeding vertebrates, the relatedness between interacting individuals is frequently measured to assess the possible importance of indirect fitness in favoring altruistic behaviors (*22*, *30*). However, in these studies, relatedness is generally measured by pedigree or with respect to the global population (giving r_{xy}), rather than with respect to competitors (r_c). If competition between relatives does occur ($r_{xe} > 0$), then the effective relatedness will be lower ($r_c < r_{xy}$), and so previous estimates of relatedness generally provide an upper limit on the value of r and the importance of indirect fitness.

Queller's (*14*) model suggests that competition between relatives can be allowed for as long as relatedness is measured at the correct scale. If relatedness is measured with molecular markers (*27*), sampling from small (local) areas could potentially do this (*14*). However, this approach has a number of drawbacks. Specifically, it (i) could mean that the value of r (e.g., for full siblings), varies within a population, over time or space, and even between different traits, possibly leading to confusion; (ii) could not be applied when pedigrees are used to estimate r; and (iii) would be methodologically difficult to apply when competition occurs to different degrees (or likelihood) between different individuals, meaning that there is no simple base population with respect to which relatedness could be measured (*31*).

An alternative method that could avoid these problems is to measure relatedness with respect to the global population, as is usually done in empirical studies (r_{xy}; e.g., full siblings give $r = 0.5$), but to then (i) allow that it is an upper estimate of the relevant r, and (ii) whenever possible, weight this parameter by some factor that allows for the amount of competition between relatives. One way to do this is to rearrange Eq. 1 to give $r_{xy}mb - c > 0$, where $m = (1 - r_{xe}/r_{xy})/(1 - r_{xe})$ (again assuming that $b = c + d$). This is Hamilton's rule with the relatedness term (r) expressed as $r = r_{xy}m$. The parameter m is the effect of competition between relatives, and is the amount by which the relatedness measured with respect to the global population (r_{xy}) needs to be multiplied to give the effective relatedness in Hamilton's rule (r or relatedness measured with respect to competitors, r_c). If there is no competition between relatives ($r_{xe} = 0$), then $m = 1$, and the standard global estimate of relatedness gives the correct r ($r = r_{xy}$). As the amount of competition between relatives increases (higher r_{xe}), m and hence the effective relatedness (r) are reduced (Fig. 1).

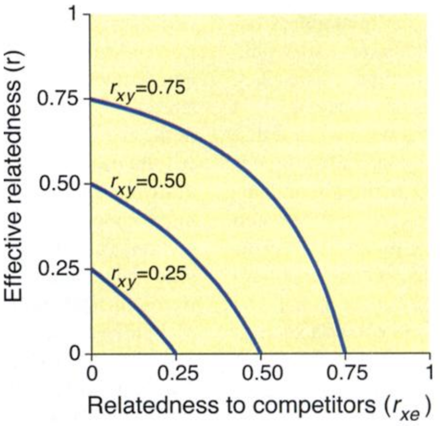

Fig. 1. Competition between relatives reduces kin selection for altruism. The effective relatedness between the actor and the benefactor (r in Hamilton's rule) decreases as the relatedness between the actor and the benefactor's competitors (r_{xe}) increases. The different lines represent different values of r_{xy}, relatedness measured by pedigree or with respect to the global population (which is equivalent to the effective relatedness, r, in the absence of competition between relatives). Empirical estimates of relatedness typically give r_{xy} and not r—the unknown quantity is how often will they differ, and by how much.

Competition and b

Frank (*4*) has developed another method for incorporating competition between relatives into Hamilton's rule, which emphasizes the role of population demographics. His method expresses the marginal benefit of increased altruism, b, as a function of three parameters: $b = B - a(B - c)$. Here, B is the benefit that would accrue to the recipients if they did not compete with each other, and it is implicitly assumed that relatedness is measured with respect to the global population (i.e., the relatedness term is r_{xy}). The parameter a is the spatial scale at which competition occurs. An increase in the reproductive success of neighbors by a proportion x increases local competition by a factor ax, but has negligible effect on the intensity of global competition. This is equivalent to Eq. 1, with $b = c + d$, and $r_{xe} = ar_{xy}$, in which case a can be interpreted as the probability that two competitors come from the same patch. If competition is completely global ($a = 0$), then any competition between relatives is negligible, and so the classic equation for Hamilton's rule holds. As competition becomes more local (increasing a), the amount of competition between relatives increases, reducing the kin selection advantage in being altruistic.

The advantages of this method are that in some cases it can be simpler to think about how the benefits of an altruistic act (rather then relatedness) change with the scale of competition, and that it provides a general methodology for incorporating competition between relatives into a range of theoretical models. As with Queller's method, Frank's model can be arranged to provide a weighting term $m = (1 - a)/(1 - r_{xy}a)$. Clearly, similar demographic extensions of Hamilton's rule, but with other parameter's (e.g., patterns of dispersal, adult survival, fertility) would be useful. Ideally, we might hope for a simple rule of thumb based upon a small number of easily estimated parameters, but this may be unreasonable given the importance of life-history details (*32*).

Rash Generalizations

How is the importance of competition between relatives likely to vary across taxa? It is clear that some generalizations can be made for extreme cases. Competition between relatives can be so extreme that it completely negates any kin selection for altruism [e.g., as is the case when male fig wasps compete for mates (*33*, *34*)]. However, there are also situations in which competition is so global that there is likely to be negligible competition between relatives. This would be the case when there is a dispersal stage between the possibly altruistic behavior and competition. For example, in many social insects (ants, bees, wasps) the reproductives (queens) disperse relatively long distances before initiating new colonies (*5*, *35*); when birds disperse large distances after fledging from their natal nest, then any competition between related adults will be negligible, and so the standard pedigree relatedness coefficients will apply when considering parent-offspring conflict and within-brood competition. We suggest that many of the most quantitatively successful areas of kin selection theory represent extreme cases in which competition between relatives is negligible [e.g., conflicts within colonies of social insects such as worker policing (eliminating eggs laid by workers), and sex allocation (*34*)]. In these areas, theory usually has ignored competition between relatives of the form we have discussed here, but luckily it turns out that it does not matter!

However, many situations will fall somewhere between these extremes, and so the importance of competition between relatives will need to be quantified empirically. For example: (i) in cooperative breeding mammals and birds, there is potential for substantial competition between relatives, such as when individuals compete for dominance and breeding opportunities within a group, but the importance of this is likely to vary substantially across species, and even between sexes of the same species (*36*, *37*); (ii) in some social insect species (e.g., subterranean termites, some ants), new nests are produced by colony budding, which can lead to competition between colonies with related queens (*5*, *38*); (iii) the relation between infection level and transmission success in many parasites suggests an intermediate position between the extremes of local and global competition (*39*); (iv) bacteria, such as *Rhizobia* in the soil, may often have dispersal patterns similar to those in the limited-dispersal models where competition between relatives exactly cancels the effect of increased relatedness (*40*). The crucial point in these cases is that simple estimates of relatedness between individuals (e.g., within social groups) can overestimate the importance of kin selection. To take an extreme example, groups of naked mole-rats (*Heterocephalus glaber*) consist of extremely close relatives (e.g., $r_{xy} = 0.8$*), and this has been taken as support for kin selection models for the evolution of cooperative breeding (41)*. However, dispersal is very limited in this species, leading to considerable potential for competition between relatives, and so the effective relatedness could be much lower (i.e., $0 \leq r_c \leq 0.8$). It has yet to be seen to what extent competition between relatives can explain cases where kin selection theory has been relatively less successful (*34*).

Conclusions

Competition between relatives can reduce and even remove kin selection for altruism toward relatives. The extent to which this can fundamentally alter our understanding of nature has been demonstrated by recent work on fig wasps (*33*). The level of fighting between males was a textbook example of the importance of kin selection—less fighting was thought to occur in species where competing males were more highly related (*19*, *21*). However, competition between relatives is so intense that it removes any kin selection for less fighting among close relatives, and fighting levels are actually explained by the direct benefit of winning any fight (males fight more aggressively when there are fewer females to compete for within a fruit) (*33*).

Hamilton argued that the influence of competition between relatives on the evolution of altruism, especially in viscous populations, was an area in which there was still much confusion [e.g., (*42*), pp. 264–265]. The theoretical work discussed here has clarified this area conceptually, and shown that kin selection theory and Hamilton's rule are correct, but that care must be applied when applying them. Although our discussion has been phrased in terms of altruism, competition between relatives has the same effect in all areas where kin selection theory can be applied (e.g. aggression, cooperative breeding, dispersal, parasite virulence, sex allocation). Indeed, essentially the same problem and equivalent results have arisen repeatedly in these fields (*4*, *14*, *20*, *34*, *43–46*). The major outstanding problem is to estimate the importance of competition between relatives empirically. However, this is not merely a problem for empirical workers—theory developed with the specific aim of helping empirical research would be extremely useful.

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24. This pattern matches that in one of the two scenarios that have been suggested for the evolution of eusociality in insects—the subsocial route (offspring remain in the natal nest to help rear their siblings)—but not in the other, the semisocial route (members of the same generation form aggregations and some individuals become helpers) (*13*).
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28. We focus on Hamilton's rule hereafter because it is an excellent conceptual tool that can be applied to any situation. However, we note that when analyzing specific cases it is usually conceptually and technically easier to start with an equation for direct fitness based upon the relevant biology, and then derive predictions (*4*, *44*). Hamilton's rule in some form usually appears as a consequence, and can be very useful for interpreting the results (*4*, *32*).
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31. For example: (i) In cooperatively breeding vertebrate species, the amount of competition between individuals will vary with a number of factors such as sex, age, and status (subordinate/dominant and natal/immigrant), as well as the group to which they belong (*36*); (ii) populations of parasites may show structuring at many levels (e.g., host, house, village), which leads to different probabilities of individuals from different hosts competing; (iii) with *Rhizobium* bacteria in the soil, the likelihood of competition between individuals for resources or infecting a new plant root will vary with the distance between them. Using genetic markers to measure relatedness with respect to competitors (r_c) in such cases would therefore require that individuals be weighted, and this would have to be done separately for each individual!
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47. We thank D. Allsop, F. Balloux, A. Buckling, T. Clutton-Brock, K. Copren, F. Denison, S. Frank, S. Gandon, T. Kiers, L. Keller, D. Queller, J. Pepper, B. Thorne, and F. Weissing for useful comments. Funding was provided by the Biotechnology and Biological Sciences Research Council and Natural Environment Research Council.