Quick guide

Kin selection

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What is kin selection? Kin selection is a part of natural selection. Selection normally favors a gene if it increases reproduction, because the offspring share copies of that gene, but a gene can also be favored if it aids other relatives, who also share copies. It is this selection via relatives that is referred to as kin selection.

How does kin selection favor altruism? Altruism is favored when Hamilton's rule is satisfied: $rB - C > 0$. Here, C is the fitness cost to the altruist and B is the fitness benefit to the individual helped. The genetic relatedness, r, devalues B according to the degree that the beneficiary shares the altruist's genes.

How can individuals calculate relatedness? They generally don't need to, any more than a bird needs to calculate aerodynamic forces to fly. If, under certain conditions, performing a behavior satisfies Hamilton's rule, then the action is favored. The triggering conditions may include cues to relatedness, which are usually based on social experience. A bee, for example, learns the smell of her birth colony — where everyone is her relative — and uses that information for classifying unfamiliar individuals.

How do we know kin selection works? First, its logical soundness is supported by a large body of mathematical theory. Second, breeders used kin selection effectively even before it had a name. As Darwin knew, even if you have to kill a cow to see if it tastes good enough to select for reproduction, you can still select its good taste by breeding its relatives. Finally, Hamilton's rule has made successful predictions about social adaptations. Particularly striking is the successful prediction that ant, bee and wasp workers should rear a sex ratio of siblings biased 3:1 towards sisters, because in these haplodiploid species they are related by 3/4 to sisters and by 1/4 to brothers.

Does the unusually high 3/4 relatedness explain the evolution of altruistic social insects? This idea of Hamilton's seemed to account for why altruistic sterile castes were common in the haplodiploid Hymenoptera compared with normal diploid species, where relatedness is 1/2 to all siblings. But once you factor in the 1/4 relatedness to brothers, relatedness among siblings in haplodiploids is not especially high. Moreover, in reality, it is usually below the maximum of 3/4 owing to multiple queens or multiple mating.

So kin selection fails to explain social insects? Wrong. Extra-high relatedness was apparently not essential, but some relatedness was. Remember, kin selection also involves the costs and benefits. Raising three half-siblings ($r = 1/4$) is better than raising one offspring ($r = 1/2$).

Should relatives ever fight? Yes. For example, in any zero-sum game ($B = C$), an individual will always be favored to prefer itself over a relative. When a queen vacancy occurs in a colony of normally cooperative honeybees, it's a zero-sum game for the candidate queens and they fight to the death even though they are sisters.

Does kin selection matter to cell and molecular biology? Yes, if for no other reason than the fact that multicellular organisms evolved because of the high relatedness among cells (usually single clones, though multicellular *Dictyostelium* can be mixtures of clones). Kin selection should affect any interactions among related pathogens, including many that determine virulence. Finally, the leading theory of the function of genomic imprinting is based on the fact that genes inherited from the mother or from the father may have different optimal kin selection strategies.

Where can I find out more?

Bourke, A.F.G. & Franks, N.R. (1995). Social Evolution in Ants (Princeton University Press, Princeton).

Queller, D.C. and Strassmann, J.E. (1998). Kin selection and social insects. Bioscience *48*, 165-175.

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Figure 1. In social insects such as these *Apoica* wasps, some individuals altruistically give up their reproduction in order to help their relatives reproduce. (Photo by Colin R. Hughes.)