EVOLUTIONARY BIOLOGY

Beyond Hamilton's rule

A broader view of how relatedness affects the evolution of altruism is emerging

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Why do worker bees give up their own reproduction in favor of other offspring of the queen? Does this make sense from a Darwinian point of view, which prescribes maximization of reproductive success? Ever since Darwin, evolutionary biologists have time and again revisited this problem of how social behavior evolved. There must be some benefit to the donor in terms of fitness, otherwise the trait would vanish. However, how to evaluate this fitness benefit remains controversial because confusion about which models to use abounds.

Most experts in evolution agree that the first detailed, and essentially correct, explanation for altruistic behavior was given by Hamilton in 1964 (*1*). Hamilton aimed to determine the conditions that allow altruistic behavior to spread. The altruist (the worker bee) cooperates by giving a benefit *b* to the recipient (other offspring of the queen) at a

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cost *c* to itself; both *b* and *c* are measured in terms of fitness, e.g., the expected number of offspring. One can trivially guess that $b > c$ must hold, but this is not enough. Hamilton's insight was that relatedness (degree of kinship) *r* between donor and recipient must enter the equation. Thus, Hamilton's rule (HR) is $br > c$.

HR is derived from what many think in turn to be maximized in evolution: the inclusive fitness of an organism. Inclusive fitness underlies kin selection, namely, it is the number of offspring equivalents in the following sense: An actor is causally responsible for some fitness contributions to all other individuals whom it has helped, at the cost of lowering its own fitness by *c*. Inclusive fitness is the weighted sum of all these additive contributions, with the weights being the relatedness values between the actor and the recipients. This approach has been applied far beyond social insects. For example, all somatic cells in a human body are maximally related to each other; this is how reproductive division of labor could evolve, so that only the germ cells make it to next generation.

In the eyes of many, HR comes close to what physicists would call a natural law. However, Nowak *et al.* have argued that HR "almost never holds" (*2*). This extraordinary

Unrelated individuals voluntarily collect garbage, adhering to the social norm that it is desirable to keep the environment clean. Recent research investigates how such norms and behaviors spread in populations.

claim has created much debate. Four recent insightful papers (*3–6*) shed more light on the evolution of cooperation, kin selection, and the role of relatedness in the evolution of cooperation. They indicate that HR has no fundamental role unless interpreted in causal terms (*3*, *6*), tackle issues associated with the notion of inclusive fitness and the role of relatedness in general (*4*), and reveal that group selection cannot always be reduced to kin selection, and vice versa (*5*, *6*).

As Birch and Okasha (*3*) explain, researchers have inadvertently been arguing about different versions of HR that are not directly comparable. The authors introduce a distinction between different versions, of which we consider only two: the special case (HRS) and the general case (HRG). These versions both use the same form of HR ($br > c$), but each has a different interpretation of the parameters *b* and *c*. In HRS, costs and benefits stem from the payoff matrix describing evolutionary encounters: who gets how much in terms of fitness upon meeting with partners of the same or other types, exactly as in Nowak *et al.*'s work (*2*). In contrast, HRG obtains *b* and *c* values by applying a statistical approach to the full model of a population.

If the payoffs are additive, as in Hamilton's original paper, then HRS is exact. Because additive payoffs are islands in an ocean of nonadditive ones, one may say that HR "never holds." If the payoffs are nonadditive then one can always design a particular

rule for each case to determine the conditions for cooperation to evolve. However, it is not ensured that a simple, elegant, and intuitive inequality such as HR will result. Other complications against mathematical elegance arise when taking into account the structure of the population, which in turn can require different definitions or interpretations of relatedness.

An apt picture of HR can be drawn by an analogy (7). If Earth were flat, a two-dimensional (2D) map would be absolutely accurate, and a straight line drawn between two cities would in fact give the shortest path between them. However, Earth is embedded in three dimensions, and 2D maps, by any cartographic projection, cannot be fully accurate. As anyone who flies on planes can tell, paths of jets (say, between Amsterdam and Boston) tend to look curved in the airline brochures, giving the false impression that jets spend more fuel and time than needed. But the shortest lines on a curved surface tend to look curved on a flat surface. Despite this distortion, flat maps can be very useful. For example, there is little inaccuracy of distance between two cities that are close to each other (like London and Amsterdam).

When scientists seek to find the right expression of relatedness so that an HR-like rule holds, they do something like finding the shortest path on a 2D map of a curved surface, depending on the projection used. Similarly, in the HRG approach (8, 9), the parameters b and c are statistical estimates and HR holds by construction (3, 4) because it is always possible to fit by regression, even if poorly, a linear model from a full population model that gives b and c. Because of the statistical nature of HRG, these estimates of b and c are not causal factors. Instead, the estimates depend on the whole population (9), including its structure (who interacts with whom in the spatial sense), so that the inclusive fitness concept is neither applicable nor enlightening. Consequently, we do not know, for example, what would happen if the particular population structure or the interactions were altered. Because HRG builds on correlations, and correlation does not necessarily imply causation, the method is blind to certain artifacts (10).

The fact that both HRS and HRG suffer from shortcomings does not prompt researchers to abandon the core idea that genetic relatedness is nonetheless important. HR may fail, but the effect of r can still be significant. In general, one should ask whether, in a given setting, the success of cooperation goes up with r or not. Van Veelen et al. have shown recently that in many cases it does (4), but evolutionary "success" can be understood in differ-

ent ways. Take, for example, a game theory approach that describes whether an actor invests in cooperation, as in Hamilton's (1) or Nowak et al.'s (2) models. Assume that the payoff values of the game, which express the individual fitness of cooperators (C) and defectors (D), are affected by their relatedness in a population. The first effect is that the rate of evolution of C, i.e., the velocity of increase in the relative frequency p of C across generations, increases with r, particularly when the initial cooperator frequency is low. That is, cooperators grow faster than defectors. Secondly, the range of initial conditions that allow cooperators to establish themselves may also increase with r. Finally, the average fitness in the population may also go up with r (4).

Further controversies arise because in some classic models, the same conclusion regarding the fate of the altruistic individuals can be reached by invoking either kin selection (KS) or group selection (GS). Group selection acts when individuals are assorted into groups, interact locally (so that their viability depends on group composition), and in subsequent steps either disperse into a global population or randomly re-

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group; the groups themselves may also split into "daughter" groups. Under group selection, fitness has an individual and a group component. For example, the fitness of an individual bird in a flock is proportional to how many chicks it has; groups of individuals then randomly form and, upon migration, the size of the flock determines the probability of survival of the group as a whole. In certain cases, this partitioning of fitness into two levels—e.g., individual reproduction and group viability—can be post hoc rewritten in one-level inclusive fitness terms. As a result, many have concluded that the equivalency between kin and group selection (KS = GS) must be completely general (3).

However, interesting group selection cases are more complex than the minimal models used to argue about KS = GS, casting further doubts about their equivalency: For many populations of molecular replicators, microbes, or indeed hunter-gatherer tribes that split and regroup, there are no neatly separated steps of group splitting, extinction, and

regrouping—necessary conditions for KS = GS (5). These component processes can occur at any instance of continuous time in the different groups. In this case, Simon (5) has shown that inclusive fitness cannot be computed without first considering group effects. That inclusive fitness can only be computed post hoc renders the kin selection approach, in these cases, futile. Moreover, inclusive fitness analyses of asynchronous group dynamics cannot provide a dynamically sufficient model to predict what happens in the long run, whereas well-constructed group selection models do exactly that (11). As Okasha has shown, in such cases, causal path analysis (6) reveals that group fitness influences individual fitness directly, rather than the other way round. This finding reinforces the point that causation is more important than mere correlation (10).

Whether or not KS = GS is also critical for understanding the origin of the human condition. Is intergroup conflict essential for cooperation, as in a model of parochial altruism (12), or is it not? Understanding the relationship between kin and group selection can provide further insight into this fascinating problem.

The scope of HR, and the relationship between kin and group selection, are now much clearer than they were even 5 years ago. The latest analyses show that HR does not hold the fundamental role that many evolutionary biologists long thought it did. This has come at the benefit of further understanding the role of inclusive fitness and relatedness in the evolution of cooperation and altruism. At the same time, we have gained knowledge on why kin selection and group selection are not equivalent except in specific cases, with the implication that these two modes of selection describe different life histories. Regarding their occurrence in nature, more empirical tests, informed by the recent theoretical results, with careful statistics are needed for further progress. Genetic relatedness is important for social evolution; HR appears to be less important, but other techniques can come to the rescue. ∎

REFERENCES

1. W. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
2. M. A. Nowak, C. E. Tarnita, E. O. Wilson, *Nature* **466**, 1057 (2010).
3. J. Birch, S. Okasha, *BioSci.* **65**, 22 (2015).
4. M. van Veelen, B. Allen, M. Hoffman, B. Simon, C. Veller, *J. Theor. Biol.* **414**, 176 (2017).
5. B. Simon, *J. Theor. Biol.* **349**, 22 (2014).
6. S. Okasha, *Br. J. Philos. Sci.* **67**, 435 (2016).
7. M. van Veelen, *J. Theor. Biol.* **270**, 189 (2011).
8. D. Queller, *Evolution* **46**, 376 (1992).
9. A. Gardner, S. A. West, G. Wild, *J. Evol. Biol.* **24**, 1020 (2011).
10. B. Allen, M. A. Nowak, E. O. Wilson, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 20135 (2013).
11. E. Szathmáry, L. Demeter, *J. Theor. Biol.* **128**, 463 (1987).
12. J. K. Choi, S. Bowles, *Science* **318**, 636 (2007).

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