

A contrasting causal hypothesis is the following: despite the fluid population structure, people were still able to seek out and preferentially interact with kin. Each individual, while cooperating with campmates for mutual benefit, had their own kinship network spanning multiple camps, and genuinely altruistic behaviour mostly occurred within kinship networks, not across them. This is, in effect, the hypothesis that early human populations were high K , low G . Studies of contemporary hunter-gatherers show that interactions between kin from different camps are more frequent than interactions between non-kin [28]. This is hardly surprising, but it suggests the high K , low G hypothesis merits further exploration.

These examples show how K - G space can help us articulate and compare empirical hypotheses. Like Maynard Smith's original proposal, it points empirical biologists towards the questions that matter, though the questions are not quite the same as Maynard Smith's: *To what extent is genetic correlation between social partners explained by kinship? Are groups clearly in evidence, and how stable and well-bounded are they?*

We need to move away from the 1960s view of kin selection and group selection as wholly different processes. But theorists also need to move away from insisting that, because these concepts are equivalent when viewed as statistical partitions of change, one of them can be dispensed with altogether. This has led to a stalemate in which theorists from the two camps continue to disagree, but without being clear as to where the disagreement lies. We should hold on to both terms as useful labels for overlapping regions of K - G space, while being pluralistic about the methods we use to analyse the processes in those regions.

ACKNOWLEDGEMENTS

I thank Samir Okasha and Andy Gardner for their comments on a draft of this essay.

REFERENCES

1. Maynard Smith, J. (1964). Group selection and kin selection. *Nature* 200, 1145–1147.
2. Hamilton, W.D. (1964). The genetical evolution of social behaviour I and II. *J. Theor. Biol.* 7, 1–52.
3. Wilson, D.S. and Wilson, E.O. (2007). Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.* 82, 327–348.
4. Lehmann, L., Keller, L., West, S., and Roze, D. (2007). Group selection and kin selection: two concepts but one process. *Proc. Natl. Acad. Sci. USA* 104, 6736–6739.
5. West, S.A., Griffin, A.S., and Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* 20, 415–432.
6. West, S.A., Griffin, A.S., and Gardner, A. (2008). Social semantics: how useful has group selection been? *J. Evol. Biol.* 21, 374–383.
7. Gardner, A. (2015). The genetical theory of multi-level selection. *J. Evol. Biol.* 28, 305–319.
8. Price, G.R. (1972). Extension of covariance selection mathematics. *Ann. Hum. Genet.* 35, 485–490.
9. Wilson, D.S. (1975). 'A Theory of Group Selection', *Proc. Natl. Acad. Sci. USA* 3, 143–146.
10. Hamilton, W.D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. In Fox, R., editor, *Biosocial Anthropology* (New York: Wiley), pp. 133–155.
11. Queller, D.C. (1992). A general model for kin selection. *Evolution* 46, 376–380.
12. Birch, J. (2017). *The Philosophy of Social Evolution* (Oxford: Oxford University Press).
13. Hamilton, W.D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature* 228, 1218–1220.
14. Birch, J. and Okasha, S. (2015). Kin selection and its critics. *BioScience*, 65, 22–32.
15. Okasha, S. (2016). The relation between kin and multi-level selection: An approach using causal graphs. *Br. J. Philos. Sci.* 67, 435–470.
16. Okasha, S. (2006). *Evolution and the Levels of Selection* (Oxford: Oxford University Press).
17. Birch, J. (2014) Hamilton's rule and its discontents. *Br. J. Philos. Sci.* 65, 381–411.
18. Okasha, S. and Martens, J. (2016). The causal meaning of Hamilton's rule. *R. Soc. Open Sci.* 3, 160037.
19. Birch, J. (2018). Kin selection, group selection, and the varieties of population structure. *Br. J. Philos. Sci.* <https://doi.org/10.1093/bjps/axx028>.
20. Fortunato, S. (2010). Community detection in graphs. *Phys. Rep.* 486, 75–174.
21. Gardner, A. and West, S.A. (2010). Greenbeards. *Evolution* 64, 25–38.
22. Michod, R.E. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality* (Princeton, NJ: Princeton University Press).
23. Queller, D.C. (2000). Relatedness and the fraternal major transitions. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 355, 1647–1655.
24. Wilson, E.O. and Hölldobler, B. (2005). Eusociality: Origin and consequences. *Proc. Natl. Acad. Sci. USA* 102, 13367–13371.
25. Hill, K.R., Walker, R.S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., Marlowe, F., Wiessner, P., and Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 337, 1286–1289.
26. Bowles, S. and Gintis, H. (2011). *A Cooperative Species: Human Reciprocity and Its Evolution* (Princeton, NJ: Princeton University Press).
27. Wilson, E.O. (2012). *The Social Conquest of Earth* (New York: W.W. Norton and Co.).
28. Hill, K.R., Wood, B.M., Baggio, J., Hurtado, A.M., and Boyd, R.T. (2014). Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PLoS One* 9, e102806.
29. Marshall, J.A.R. (2011). Group selection and kin selection: formally equivalent approaches. *Trends Ecol. Evol.* 26, 325–332.

Department of Philosophy, Logic and Scientific Method, London School of Economics and Political Science, Houghton Street, London, WC2A 2AE, UK.
E-mail: j.birch2@lse.ac.uk

Primer

Kin selection and altruism

Tomas Kay, Laurent Lehmann, and Laurent Keller

"You cannot divorce kin selection from neo-Darwinism, any more than you can divorce the Pythagorean theorem from Euclidean geometry."

*Richard Dawkins,
An Appetite for Wonder*

Natural selection is predicated on the 'struggle for existence': life is short, cruel and, whether through predation, disease or starvation, often ends traumatically. It would seem that in such a dog-eat-dog world, organisms ought to act selfishly, and avoid reducing their fitness (expected survival and reproductive success) by expending time and energy helping others. Put another way, alleles that increase the probability of altruism — a behavior whose expression increases the fitness of recipients while decreasing that of the actor — should decrease in frequency across generations and ultimately disappear.

But altruism as so defined is prevalent in nature (Figure 1). One type of such apparently paradoxical behavior is documented in over 220 bird and 120 mammal species, where self-sacrificing individuals forego reproduction to assist other group members. In these taxa, altruists are typically young individuals who help their parents to rear their younger siblings. A more extreme case occurs in social insects, where some individuals, the 'workers', irreversibly commit themselves to sterility (Box 1). Some ant species form colonies with in excess of a million sterile workers specialized on tasks such as nursing the young, foraging for food and defending the nest, while reproduction is restricted to one or few queens.

The notion of self-sacrifice to help others has long attracted attention. It is extolled by all major religions (for example, "thou shalt open thine hand wide unto him, and shalt surely lend him sufficient for his need",



Deuteronomy 15:8) and discussed by eminent philosophers: lauded by some (for example, “the moral law causes the people to follow [their leader] regardless of their lives, undismayed by any danger.”, Sun Tzu) while derided by others (for example, “to choose instinctively, what is harmful to *yourself*, to be *tempted* by ‘disinterested’ motives, this is practically the formula for decadence... people are done for when they become altruistic”, Nietzsche). The same notion has perplexed both economists and biologists. Darwin was aware of the problem that the existence of sterile workers posed to natural selection, terming them his “one special difficulty”. He devoted significant time to documenting altruistic behaviors and, with remarkable prescience, noted that: “the difficulty, though appearing insuperable, is lessened, or as I believe disappears when it is remembered that selection may be applied to the family”. Despite Darwin’s attention, the evolutionary explanation of altruism remained obscure until W. D. Hamilton provided a pivotal insight.

To understand the genetic evolution of any trait, it is important to consider the average fitness of all individuals in the population bearing an allele responsible for producing a change in that trait value. Hamilton pointed out that a help-inducing allele will increase in frequency when $rb - c > 0$, where $-c$ is the average effect of the help-inducing allele on the fitness of its bearer, b is the average effect on the fitness of recipients and r is the genetic relatedness between actor and recipients. The relatedness coefficient r measures the extent to which a recipient of helping is more likely than a random individual in the population to carry the help-inducing allele. This elegant formalization emphasizes how an allele resulting in a fitness cost to its bearer ($c > 0$) can nevertheless be favored by selection if the correlated fitness benefits on other bearers of the allele ($rb > 0$) outweigh the cost. Imagine two siblings. On average they have a 50% chance of having inherited the same allele at any given locus (full sibling relatedness = 0.5). An allele that induces an altruistic behavior

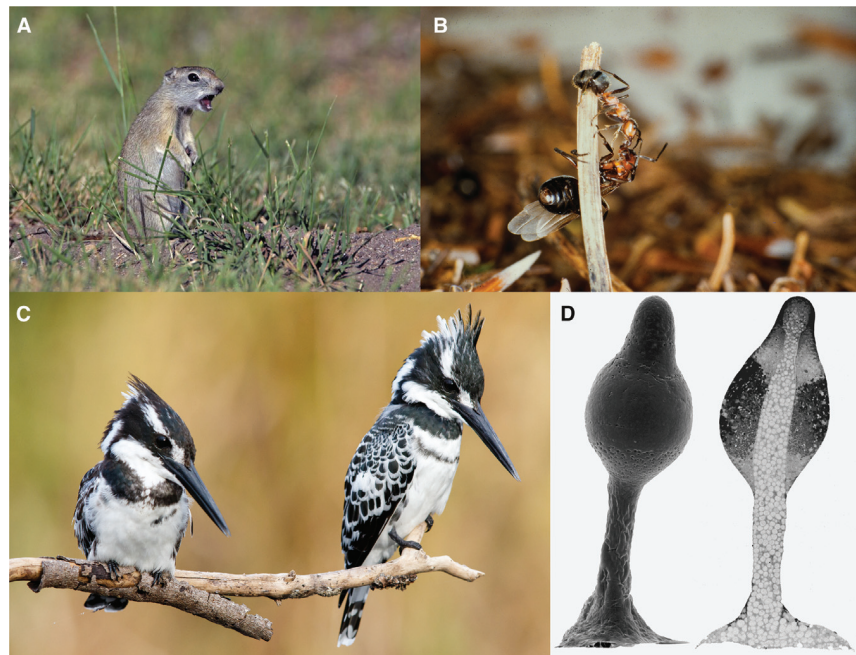


Figure 1. Paradigmatic examples of altruistic phenotypes explained by kin selection.

(A) An alarm-calling Belding’s ground squirrel. Squirrels emit costly calls more frequently when surrounded by a higher proportion of relatives. (B) Two *Formica* ant sisters (a worker and a queen) who differ markedly in morphology, longevity and reproductive potential. Sterile workers have only evolved in highly related groups. (C) Pied kingfishers. In this species, young individuals often ‘stay at home’ to help their parents rear younger siblings. Relatedness determines both who individuals help and the amount of help provided. (D) A multicellular slime mold fruiting body (left: SEM; right: light micrograph cross-section). The once free-living cells in the stem sacrifice their reproductive success to increase that of other cells. Relatedness in these structures is typically very high. Photographs are reproduced courtesy of (A) Ron Wolf; (B) Laurent Keller; (C) Johan Kok; and (D) Richard Blanton and Mark Grimson.

between siblings will therefore spread if the benefit to the recipient sibling is at least twice the cost to the acting individual.

A key feature of Hamilton’s original (1964) model is its frequency-independence: under weak selection, that is where phenotypic differences have small fitness effects, $rb - c > 0$ holds for all population frequencies of the allele increasing altruism. Hamilton referred to this consistency as “a gift from God” because it means that the same rule explains both the initial spread of a new allele *and* its eventual fixation in the population. The rule can therefore be applied to successive mutations elaborating a trait, thereby explaining the gradual evolution of quantitative altruistic phenotypes. An equilibrium is reached when $rb - c = 0$, which provides a defining and practically useful characterization of an evolutionary stable phenotype. The frequency-

independence of Hamilton’s rule at the allele level applies to all quantitative phenotypes under weak selection, and has been shown to even hold when the phenotypes of actor and recipient interact (as under any realistic social interaction) and in demographically complex and spatially structured populations. This is miraculous because intuitively one would expect frequency-dependent phenotypes to result in frequency-dependent selection, under which gradual Darwinian evolution is likely to break down.

The true generality of Hamilton’s rule is rarely understood. Kin selection is sometimes thought of as an esoteric counterpart to natural selection, useful only for understanding interactions within family units. The reality is that in any population where dispersal is limited in space, even to the slightest degree, interacting individuals will have $r > 0$

Box 1. Kin selection and eusociality.

The most extreme altruism in nature is observed in eusocial insect colonies, where one or few individuals produce all offspring, while others are permanently sterile. Hamilton initially conceived kin selection as a framework to understand the evolution of such a fascinating system. Broadly, this is now understood: In a monogamous population, individuals are, on average, as related to siblings (0.5) as they are to their own offspring (0.5). Consequently, under this mating system, if the benefit of helping at the maternal nest (b) is greater than the cost of forgoing reproduction (c), selection will favor reproductive altruism. The ratio of $b:c$ depends on a number of ecological parameters including the mortality rate, the ease with which a new nest can be founded, and the availability of resources within the maternal nest. At the genetic level, an allele which always induces sterility can never spread. Instead, sterility must be expressed probabilistically. Thus, sterility is likely to be a quantitative phenotype that can evolve gradually by small, stepwise transformations caused by allelic substitutions. In social insects, caste fate is typically determined environmentally, for example based on larval diet, and not genetically. There are, however, special cases where caste fate is entirely genetically determined. Some *Messor* and *Pogonomyrmex* harvester ant species, for example, comprise two interdependent genetic lineages. Queens mate with males of both lineages, and pure-lineage eggs develop as new queens while mixed-lineage eggs develop as workers. Here, while caste is genetically determined, it is not particular alleles which bias development but rather heterozygosity, or particular allelic combinations at different loci.

and phenotypic evolution will be affected by the indirect component of fitness (rb). This applies to any trait, but particularly to social ones, like inbreeding avoidance, dispersal strategies, competitive traits or sex-ratio evolution. Further, kin selection subsumes classical natural selection, which represents the special case where all interacting individuals are completely unrelated ($r = 0$) so only the direct fitness effect ($-c$) matters for selection. Additionally, because Hamilton's rule reconciles gradual Darwinian evolution with particulate Mendelian inheritance for all traits, it bolsters the modern synthesis and extends it to the realm of social interactions. The rule therefore unifies social evolution with quantitative genetics, ecology and long-term adaptive dynamics by providing a simple description of the direction of microevolution under weak selection. As details of genetic underpinnings can be omitted, the rule is readily applicable to behavioral ecology and social evolution.

Following Hamilton's key insight, there has, unfortunately, been substantial confusion surrounding the term altruism. Trivers coined the term 'reciprocal altruism' to describe how seemingly altruistic behavior can evolve over reciprocal interactions (in

which partners alternately help one another). But behaviors with a short-term loss and long-term gain are not truly altruistic as they increase the actors Darwinian fitness. Further work showed 'reciprocal altruism' or, more accurately, 'reciprocity' to be one of many mechanisms for the evolution of non-altruistic cooperation (a behavior whose expression increases the fitness of recipients and that of the actor). Other mechanisms include cooperation as the by-product of a self-interested act, and enforced cooperation through the punishment of non-cooperation. In all these cases, cooperation readily evolves because it provides direct fitness benefits ($-c > 0$). Importantly, there is currently not a single theoretical model which shows that altruism can evolve between unrelated individuals.

Further confusion arose because some authors misunderstood the kin selection model or wrongly claimed to have found an alternative situation conducive to the evolution of altruism. This is well illustrated by the group selection *versus* kin selection controversy. The general idea of group selection models is to use a multi-level approach to partition selection into components of within group and between group selection. Contrary to what is sometimes

claimed, however, group selection models are not fundamentally different from classical kin selection models and it is possible in every instance to translate one approach to the other without disturbing the mathematics describing the net result of selection.

Other examples include the so-called spatial, lattice, or evolutionary graph models, where individuals are positioned on a grid (or represented as nodes in a network) and interact with nearest-neighbors to produce offspring which disperse locally. Here too, authors have claimed novelty, but once the mathematical or simulation smoke-screen is blown away, the life-cycle assumptions of these models often entail altruistic interactions occurring exclusively between siblings or parent-offspring pairs. Thus, the outcome of these models is merely a less general reincarnation of Hamilton's original insight.

A good theory must provide novel predictions and fit with data. Kin selection has performed remarkably well, as illustrated by the following paradigmatic examples. In birds and mammals, individuals are more likely to warn relatives about the approach of a predator. For example, when groups of Belding's ground squirrels are threatened, some individuals stand on their hind legs and emit a high-pitched squeak. Callers likely incur a cost by increasing their conspicuousness. Individuals are more likely to give these alarm calls when surrounded by close relatives. Moreover, females call more frequently than males, which makes sense given that dispersal is male-biased resulting in higher relatedness of females than males to neighbors.

Cooperative breeding is broadly restricted to kin-based groups. Under monogamy, a focal individual's relatedness to siblings is as high as to its own offspring. As polygamy increases, an individual's relatedness to siblings decreases. Accordingly, across over 250 bird species, cooperative breeding is associated with low promiscuity, and in cooperatively breeding species, the level of helping covaries with promiscuity. In pied kingfishers, for example, relatedness determines both whom an individual helps and the

amount of help provided. Additionally, across species with intermediate levels of promiscuity, the strength of kin discrimination increases with the benefit of helping *b*.

Numerous phylogenetic analyses have revealed that the major evolutionary transition to eusociality in Hymenoptera (ants, bees and wasps), as well as cooperative breeding in vertebrates, evolved in highly related (mother–offspring) groups. There are exceptional ant species in which relatedness between nestmates is low; however, this results from a secondary increase in queen number long after the evolution of worker sterility. Monogamy is also the rule of thumb in termites, where multiple breeders occur only in evolutionarily derived lineages. In both termites and eusocial Hymenoptera the benefit of raising siblings instead of offspring typically comes from the increased nest-defense capability of larger groups, or insurance against the mortality of any single care-giver.

Although high relatedness favors altruism, potential conflicts persist in kin groups because group members are not genetically identical and may attempt to favor the propagation of their own genes at the expense of other group members. Conflict can occur over access to reproduction or over resource allocation among group members. Paradoxically, while kin selection was proposed to explain the evolution of altruism, the outcomes of within-group conflict provide some of the theory's most compelling evidence. For example, kin selection predicts that in social insect colonies relatedness determines the value of new queens and males to other colony members. Social Hymenoptera have a haplodiploid system of sex-determination, where unfertilized (haploid) eggs develop as males whereas fertilized (diploid) eggs develop as females. Under this system, full worker sisters share half of their maternally inherited genes, and all paternally inherited genes. With brothers, workers share half of their maternally inherited genes but never any paternally inherited genes since males have no father. Queens, however, share half of their genes with both sons and daughters. This results in genes in queens and

workers differently valuing new males and females, with workers preferring a more female-biased sex ratio. Kin selection therefore predicts a conflict between queens and workers over the colony sex ratio: consistent with this prediction, and with workers winning out, many ant species have a female-biased sex ratio, which workers achieve by selectively eliminating male brood.

Kin selection further predicts that conflict over the sex ratio should covary with the number of males a queen mates. Under haplodiploid sex-determination, multiple mating decreases the relatedness between the workers in a nest, but not between workers and their brothers. Consequently, under worker control, colonies headed by a multiply-mated queen should produce a higher proportion of males. If the queen is in control, however, the sex investment ratio should be independent of the number of times she mates as this does not influence her relatedness to offspring. This prediction was confirmed in studies comparing the colony-level sex ratios in species with variable breeding structure. In several species, workers in colonies headed by a singly-mated queen eliminate a high proportion of male brood resulting in a strongly female-biased colony sex ratio. Contrastingly, in colonies headed by a multiply-mated queen, male brood persists. This creates a population-level pattern known as a split sex ratio, with some colonies producing mostly males and others producing mostly females. There are, however, some species which exhibit no apparent association between sex ratio and colony-level relatedness. In these species, queens can apparently bias the sex ratio in their favor by, for example, limiting the number of female eggs produced. Remarkably, the predictions of population-level female-biased sex ratio and of colony-level split sex ratios were predicted *a priori* by kin selection.

For a long time, kin selection was primarily used to understand the evolution of altruism in vertebrates and insects, and that of eusocial insect colonies. Over recent years, kin selection has been applied more broadly across the tree of

life, leading to numerous advances. Some species of plant seem capable of discriminating kin from non-kin and investing less heavily in root development when pot-sharing with kin. Microbes are surprisingly social: they cooperate to perform an array of tasks including nourishment, movement, communication and the production of multicellular bodies. The microbial social landscape differs from that of vertebrates and insects because, rather than kinship categories such as full-sibling and half-sibling, the maxim is whether or not partners are clonemates.

Interestingly, several microbes have been demonstrated to discriminate based on similarity at a particular locus. For example, the bacterium *Proteus mirabilis* swarms (a type of motility) over solid surfaces. Swarming is mediated by the six-gene locus *ids*: cells carrying the same alleles swarm together while boundaries form between swarms of strains with alternative alleles. Kin selection has proven particularly useful to understanding such microbial interactions: relatedness affects diverse behaviors including nutrient uptake strategy in *Pseudomonas aeruginosa*, altruistic multicellular stalk formation in *Dictyostelium discoideum* and toxin production in *Escherichia coli*.

Kin selection was also critical to the major evolutionary transition to multicellular life. This transition is functionally analogous to the evolution of eusocial colonies, with workers representing somatic cells and queens representing the germ line. Here too, relatedness is paramount with clonal lineages being more likely than nonclonal lineages to evolve sterile cells, more likely to transition to obligate multicellularity, and typically forming multicellular bodies with both more cells and more cell types.

In conclusion, kin selection theory is one of the most significant advances in evolutionary biology since Darwin and provides a modern, gene-centered representation of natural selection. The theory was pioneered by W. D. Hamilton, and across subsequent decades biologists have clarified and vastly extended the theory and its range of application,

which, in addition to the discussed examples, includes genomic imprinting, pathogen virulence, inter-generational transfer, menopause and others. This very strong and integrative framework continues to provide exciting insights to domains far from its roots. Many remaining lacunas are mechanistic: little is currently known about how altruistic traits are produced developmentally; how they can be learned; or of their genetic architecture in eukaryotes. Further investigation along these lines will prove fruitful.

FURTHER READING

- Boomsma, J.J. (2009). Lifetime monogamy and the evolution of eusociality. *Philos. Trans. R. Soc. Lond. B* 364, 3191–3207.
- Bourke, A.F.G. (2011). *Principles of Social Evolution* (Oxford: Oxford University Press).
- Bourke, A.F.G., and Franks, N.R. (1995). *Social Evolution in Ants* (Princeton: Princeton University Press).
- Buckling, A., Brockhurst, M.A. (2008). Kin selection and the evolution of virulence. *Heredity* 100, 484–488.
- Cornwallis, C.K., West, S.A., Davis, K.E., and Griffin, A.S. (2010). Promiscuity and the evolutionary transition to complex societies. *Nature* 466, 969–972.
- Frank, S. (1998). *Foundations of Social Evolution* (Princeton: Princeton University Press).
- Gilbert, O.M., Foster, K.R., Mehdiabadi, N.J., Strassmann, J.E., and Queller, D.C. (2007). High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proc. Natl. Acad. Sci. USA* 104, 8913–8917.
- Grafen, A. (1985). A geometric view of relatedness. *Oxford Surv. Evol. Biol.* 2, 28–89.
- Haig, D. (2013). Kin conflict in seed development: an interdependent but fractious collective. *Annu. Rev. Cell Dev. Biol.* 29, 189–211.
- Hamilton, W.D. (1963). The evolution of altruistic behaviour. *Am. Nat.* 97, 354–356.
- Hamilton, W.D. (1964). The genetical evolution of social behaviour, I and II. *J. Theor. Biol.* 7, 1–52.
- Keller, L., and Surette, M.G. (2006). Communication in bacteria: an ecological and evolutionary perspective. *Nat. Rev. Microbiol.* 4, 249–258.
- Lehmann, L., and Rousset, F. (2014). The genetical theory of social behaviour. *Philos. Trans. R. Soc. Lond. B* 369, 20130357.
- Meunier, J., West, S.A., and Chapuisat, M. (2008). Split sex ratios in the social Hymenoptera: a meta-analysis. *Behav. Ecol.* 19, 382–390.
- Puurtinen, M. (2011). Mate choice for optimal (k) inbreeding. *Evolution* 65, 1501–1505.
- Queller, D.C. (2000). Relatedness and the fraternal major transitions. *Philos. Trans. R. Soc. Lond. B* 355, 1647–1655.
- Sundström, L., Chapuisat, M., and Keller, L. (1996). Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. *Science* 274, 993–995.

Department of Ecology and Evolution,
University of Lausanne, Biophore, 1015
Lausanne, Switzerland.
E-mail: tomas.kay@unil.ch (T.K.),
laurent.lehmann@unil.ch (L.L.),
laurent.keller@unil.ch (L.K.)

Primer

Public goods and cheating in microbes

Parker Smith and Martin Schuster*

Communication and cooperation are not restricted to complex, higher organisms. Microbes, too, perform a variety of collective, multicellular behaviors, including biofilm formation, quorum sensing, nutrient acquisition, and dispersal. The products of these microbial cooperative behaviors are generally referred to as public goods. Here we describe the nature of microbial public goods, the associated problem of cheating, and ways in which microbes maintain public goods in the face of cheating. We highlight work in a growing field at the interface of microbiology, evolution, and ecology that combines multiple approaches in experimental evolution, genetics, and mathematical modeling.

Public goods

The concept of public goods is rooted in economics. Examples of economic public goods are national defense, public parks, street lighting, and waste-water treatment plants. They are financed by tax revenues and are freely available to all citizens. Analogously, the defining characteristic of public goods in the context of social evolution is that they are costly to produce for the individual and are beneficial to all members of the local group or population.

In microbial cooperation, public goods are loosely defined as compounds or functions that provide a collective benefit, generally through release into the extracellular environment. Microbial public goods take many forms (Figure 1 and Table 1): They range from large proteins to small metabolites; they may be actively secreted or they may passively diffuse from the producing cell. For example, extracellular enzymes degrade polymers into smaller fragments that can be taken up by individual cells, siderophores scavenge iron in depleted environments,

biosurfactants promote group motility over surfaces, toxins injure host tissues to release nutrients, and antibiotics harm competing microbes. Exopolysaccharides and proteins form a protective extracellular matrix in bacterial biofilms, and secreted signaling molecules coordinate the behavior of the population in a process termed quorum sensing. A well-studied microbial species exhibiting all these properties is the opportunistic bacterial pathogen *Pseudomonas aeruginosa*, which is often associated with chronic infections in cystic fibrosis.

A different type of public good that is not a chemical compound is the light produced by some bioluminescent bacteria. When the bacteria form a mutually beneficial relationship with marine animals, the light serves to attract prey or distract predators. Finally, examples of more complex forms of microbial behavior are the fruiting bodies — multicellular, stalked sporangia that are formed by myxobacteria and social amoebae. Here, the entire structure may be considered the public good, as it is the product of cooperation.

Another characteristic of public goods is that their benefit generally increases with population density. This aspect is easy to understand in the context of antibiotics or secreted enzymes. Antibiotics are only effective against competitors above a certain threshold concentration and therefore require an appropriately high density of cells that contribute to antibiotic production. Similarly, as population density increases, secreted enzymes that process nutrients progressively benefit neighboring cells rather than diffuse away. These properties presumably are a major reason why the production of many public goods is controlled by quorum sensing. Quorum sensing can therefore be understood as a mechanism of facultative cooperation, where signaling with relatively cheap public goods serves to limit the production of more expensive public goods to the appropriate social and environmental conditions.

Basic features of microbial cheating

In microbial populations, public goods are readily shared, and thus they can be easily exploited by cheaters. Cheaters are non-cooperating

