

Public goods in relation to competition, cooperation, and spite

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Edited by Brian Skyrms, University of California, Irvine, CA, and approved April 11, 2014 (received for review February 10, 2014)

Public goods and common-pool resources are fundamental features of biological and social systems, and pose core challenges in achieving sustainability; for such situations, the immediate interests of individuals and the societies in which they are embedded are in potential conflict, involving game-theoretic considerations whose resolution need not serve the collective good. Evolution has often confronted such dilemmas—e.g., in bacterial biofilms—in the challenges of cancer, in nitrogen fixation and chelation, in the production of antibiotics, and in collective action problems across animal groups; there is much to learn from the Darwinian resolution of these situations for how to address problems our societies face today. Addressing these problems involves understanding the emergence of cooperative agreements, from reciprocal altruism and insurance arrangements to the social norms and more formal institutions that maintain societies. At the core are the issues of how individuals and societies discount the future and the interests of others, and the degree that individual decisions are influenced by regard for others. Ultimately, as Garrett Hardin suggested, the solution to problems of the commons is in “mutual coercion, mutually agreed upon,” and hence in how groups of individuals form and how they arrive at decisions that ultimately benefit all.

prosociality | collective phenomena | complex adaptive systems

Problems of public goods and common-pool resources arise in socioeconomic and ecological contexts alike, and have posed correspondingly similar challenges for management and for evolution (1, 2). Each discipline has dealt with them differently, and each has much to learn from the other. The central thesis of this paper is that, because evolution—genetic and cultural—has found resolution of these puzzles, Darwinian thinking can help to inform how societies might address some of its greatest issues. Indeed, the problem of sustainability, perhaps the greatest challenge facing humanity, is essentially a problem of learning to live together in the global commons, and to deal equitably and wisely with public goods and common-pool resource problems (3, 4).

The great economist Paul Samuelson defined public goods as ones “which all enjoy in common in the sense that each individual’s consumption of such a good leads to no subtractions from any other individual’s consumption of that good” (5); in that sense, they are “nonexcludable” and “nonrivalrous,” which distinguishes them technically from goods like fisheries, where the use by one individual diminishes availability to others. For the purposes of this paper, however, I will not distinguish among them, and will loosely use the term “public good” to refer to both, from truly nonrivalrous and nonexcludable items like clean air and public parks to fish, water, and other common-pool resources.

The key issue surrounding public goods and common-pool resources, in socioeconomics as well as in evolutionary and behavioral ecology, is whether individuals can suppress their selfish calculations in the interest of achieving an end result that provides collective benefits in excess of what individuals would receive if acting independently, in ways to maximize perceived short-term benefits; if they can, the resultant cooperation may leave everyone better off, or there may be winners and losers. Hence, crucial aspects that affect whether such cooperation can be achieved must

involve fundamental issues of discounting (the degree to which individuals favor short-term benefits vs. longer-term ones), prosociality (the concern individuals have for others), and collective decision-making in the presence of imperfect and generally asymmetric information. I will address each of these in turn.

Learning from Nature

The main focus of this paper, and of the special issue in which it appears, is the social sciences, and how Darwinian thinking might help us to understand why individuals do what they do in social situations, and how such inclinations can lead to cooperation in dealing with public goods. A natural place to start, therefore, is to examine how public goods and common-pool resource problems, henceforth termed “public goods problems,” have been addressed in nature. Indeed, such problems have represented fundamental challenges that evolution has confronted, sometimes, but not always, successfully (6, 7). Biological organisms produce many public goods, including knowledge and information shared in collective activities (8–10). Many organisms combine their efforts to build and maintain collective nests or hives; microorganisms chelate iron through the production of costly siderophores; plants (and especially legumes) enter into (also costly) mutualisms that allow nitrogen to be fixed, benefitting the *N*-fixers but also benefitting other plants in their neighborhoods; and many organisms produce allelochemicals, antibiotics that poison competitors but also benefit those that are resistant to the toxins but do not pay the price of producing them.

Even bacteria cooperate, and indeed provide case studies worth emulating in terms of how the collective good can be served (11). Many bacteria produce extracellular polymers; these can provide a matrix for growth as well as signals of population levels (12), making possible biofilms, cooperative arrangements among bacteria that provide collective benefits. The extracellular polymers are hence public goods, creating an evolutionary puzzle of understanding how their production, which is costly, can be sustained (13, 14). Some bacteria produce these polymers at low densities, some at high densities, some constitutively, and some not at all; the conditions that select for these various behaviors evolutionarily are amenable to the standard methods of adaptive dynamics (15), as well as tools from other disciplines (13).

Of course, similar situations, in which individuals cooperate to sustain a public good, are legion for a variety of organisms more complex than bacteria, from swarming insects to flocking birds and schooling fish, to more and more complex societies of

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, “In the Light of Evolution VIII: Darwinian Thinking in the Social Sciences,” held January 10–11, 2014, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and audio files of most presentations are available on the NAS website at www.nasonline.org/ILE-Darwinian-Thinking.

Author contributions: S.A.L. designed research, performed research, contributed new reagents/analytic tools; and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

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invertebrates or vertebrates (16). By understanding how these have evolved, we gain insight into the dynamics of social evolution in human societies.

At the other extreme of biological organization, endogenous pathogen cells produce metabolites that represent a public good, e.g., during cancer progression (17); treating cancer progression as a game between normal and malignant cells is thus natural (18, 19) and was already suggested nearly a decade ago by Axelrod et al. (20). Cancer itself of course represents a breakdown in cooperation and the maintenance of a public good (21), so the idea of developing new strategies for treating cancer—e.g., by attacking the public goods that allow cancers to thrive—seems an appropriate turnabout (17, 22, 23).

Human Societies and Public Goods

The prototypical public good is the commons we all share (3). William Forster Lloyd, a British political economist, introduced the notion of the commons nearly two centuries ago (24), and Hardin built on it in his famous paper, “The Tragedy of the Commons” (25). Hardin pointed out that the resolution of potential tragedies could emerge from “mutual coercion, mutually agreed upon,” and Elinor Ostrom and others demonstrated how effective this could be in small communities (26). Globally, the situation is much less satisfactory, as we know from the failure so far of international efforts to deal with problems like climate change (3, 27). Why? The answer lies, to large extent, in discounting of two kinds: We discount the future, and we discount the interests of others (see ref. 28).

It is natural to ask, then, how we discount, and why. How has evolution, both genetic and cultural, shaped our personal and societal discount rates? How has it shaped our concern for others? The answers to these questions to some extent require an understanding of the emergence and elaboration of groups, and the social norms, customs, and laws that become associated with those groups and help sustain them. How do individuals become organized into groups to begin with, what is the collective behavior of those groups, and how do they serve as building blocks for societies?

Discounting

Solutions to public goods problems involve various forms of cooperation, often through insurance arrangements, and the success of such arrangements rests heavily on how individuals discount the future. Temporal discounting, the phenomenon of weighting present benefits more heavily than future ones, is fundamental to how individuals and societies value things, and key to the potential for cooperative agreements and for sustaining societies and their benefits (29). In economics, the notion of present value, sometimes called present discounted value, incorporates the discount rate into a measure of the future value of an object discounted to reflect its interest-bearing potential. We discount to some extent because of uncertainty, and to some extent because, in an overall environment of growth, current benefits can be reinvested to reap even bigger rewards in the future (captured in the notion of the time value of money). However, each of us discounts differently, in ways shaped by evolution, experience, and risk tolerance. How these influences interact to shape our individual and collective patterns of temporal discounting remains to large extent a mystery, but some insights are available from evolutionary theory.

The most robust body of evolutionary theory that bears on this topic involves the notion of reproductive value, a mainstay of life history theory (30). Basically, reproductive value adds up the expected future lifetime reproductive contributions of an individual, and discounts according to the anticipated rate of population growth. Earlier reproduction events have higher value, because the offspring so produced are in the pipeline and reproducing earlier. In that sense, reproductive value is similar in concept to

that of the time value of money. Individuals with higher reproductive value will make larger contributions to future generations, and hence should be foci for strong selective pressures.

Mathematically, the concept of discounting is represented by the standard formula

$$PV = PV(0) = Be^{-\delta t},$$

expressing the notion that a benefit's present value (PV) at time 0 is equal to the actual value of the benefit (B) discounted by an amount $e^{-\delta t}$, where t is the time in the future when the benefit will be realized. When dealing with a stream of benefits, one can extend this to a formula of the form

$$PV(T) = \int_T^{\infty} B(t)e^{-\delta(t-T)} dt,$$

which captures the present value at time T in terms of a continuum of future benefits.

This standard formulation assumes that the discount rate is constant; but there is no reason that this should be the case, just as there is no reason that population growth or the time value of money should be at constant rate. Indeed, there is considerable evidence that humans, as well as other animals, use a variable discount rate $\delta(t)$, discounting the near future at a comparatively higher rate (31–37). Classically, the variable rate is assumed to follow a hyperbolic form,

$$\delta(t) = \log(1 + rt),$$

but the term “hyperbolic” is often abused to apply more generally to any variable discounting that discounts the shorter term more heavily.

Reasons why animals should discount hyperbolically vary, depending on whether one is focused on ultimate vs. proximate explanations; furthermore, hyperbolic discounting has a number of counterintuitive consequences, which raise deep problems of interpretation.

The most immediate consequence of hyperbolic discounting is intertemporal inconsistency, in which decisions made by an individual about the time period t_1 to t_2 will differ depending on when they are made; indeed, knowing this should in principle cause an individual to alter his or her decisions at the earlier time, leading to some paradoxes similar to those characteristic of time travel.

As for explanations, a place to start is from the observation that averaging independent exponential (constant rate) discount curves will yield an overall curve that is hyperbolic in the loose sense of the definition. Hence an individual making a decision that involves tradeoffs among different objectives, which will in general be weighted differently and subject to different discount rates, will end up discounting hyperbolically if he or she simply aggregates the relevant discount curves associated with these objectives. Indeed, the decisions related to different objectives might be associated with different regions of the brain; it is beyond the scope of this article to conjecture whether this differentiation involved independent evolutionary events (but see ref. 38).

The notion of averaging or aggregation of discount curves is also reflected in the dynamics of group decision-making. Weitzman writes that “the main finding is that even if every individual believes in a constant discount rate, the wide spread of opinion on what it should be makes the effective social discount rate decline significantly over time” (39).

Evolutionarily, there are a number of closely related factors that can contribute to hyperbolic discounting. Sozou (40) argues that “the value of a future reward should be discounted where

there is a risk that the reward will not be realized,” which indeed is an argument for any kind of discounting. Dasgupta and Maskin (41) emphasize, instead, the uncertain realization of the times of payoffs, a much more general concept. I would argue as well for the importance of bounded rationality (42, 43); that is, we have evolved more sensitive discriminators of nearby events, in space and in time, because we can, and this quite naturally causes us to judge more distant ones as being similarly separated in time, thus lumping them together.

Prosociality and Spite

Intertemporal discounting is only part of the story; we also discount across the networks of our interactions, including both kin and nonkin. Some of the latter is intertwined with intertemporal discounting, because it affects the intergenerational transfer of resources to our children and grandchildren (44–47), as well as what we leave to unrelated individuals and society at large. In classical evolutionary theory, the focus is on kin, and how selection is affected by the benefits one's actions bestow upon kin (48). More generally, however, individuals engage in actions that also benefit or harm nonkin, and such actions may be favored through either genetic or cultural evolution.

For the purposes of this section, I shall adopt a broad definition of prosociality, to measure the concern an individual has for the interests of others, especially as it affects the actions that individual will take; indeed, I will also apply it to individuals, like plants and microorganisms, that do not have the capability for concern, but whose actions have been selected or otherwise favored explicitly because they benefit others. In this broad sense, spite is the opposite of prosociality, because it may be represented by the same term with an opposite sign; it will apply to actions that have been favored because they harm others. Often, in the context of evolutionary investigations, the definitions of prosociality and spite alike are more strictly defined as actions that impose a cost on the actor, but this distinction will not be crucial in this section.

As we shall see, prosociality is crucial to the resolution of many public goods conflicts, and may be greatly facilitated by social structures that localize interactions; however, as we shall also see, the same also may be said about spite. I shall also use the term prosociality to include care lavished on kin, rather than distinguishing kin selection as something separate from prosocial selection more generally; furthermore, I will not attempt to distinguish true altruism, if it really exists, from behaviors shaped by the rewards and punishments societies impart.

Understanding how prosociality arises represents a fundamental challenge in behavioral economics, much as it has in evolutionary theory since the time of Darwin (49, 50). In general, contributions to public goods (and common-pool resources) can be mediated by a combination of intrinsic prosociality, as shaped by genetic evolution; reciprocal arrangements and contracts; and norms, laws, and incentive systems that may lead to prosocial behaviors. Hence understanding what factors sustain or might enhance prosociality is crucial to resolving commons dilemmas.

Understanding prosociality naturally shares many features with the classical evolutionary problem of understanding altruism, which worried Darwin a great deal as a challenge to his theory of evolution through natural selection. Debate continues among evolutionary theorists about the importance of genetic relatedness in shaping altruistic behaviors (48, 51–54), but no one would argue that close genetic relatedness is essential for cooperation; there are too many examples to the contrary, and too many well-understood mechanisms that foster cooperation. Reciprocal altruism, in which individuals enter into explicit or implicit cooperative agreements, represents one such powerful mechanism (55); indeed, population viscosity, which restricts individuals' interactions to others in their neighborhoods, can impose effective reciprocal arrangements even without individuals

being able to recognize one another. The effects of spatially limited interactions hence can lead to cooperative arrangements not only among animals, but also among plants and microorganisms. The role of effects of this sort are evident in the biofilm example already discussed (15), as well as in the cellular slime mold (56).

Numerous authors have explored simple models of competition on lattices or spatial grids, and demonstrated how spatially restricted interactions can facilitate the evolution of cooperative behavior (57–60). In typical simulations, in the places where cooperators are by chance initially in higher concentrations, everyone does better, leading to the spread of cooperative behaviors. Another possibility, when movement to or births onto contiguous sites is allowed, is that cooperators and defectors will coexist in a spatiotemporal mosaic. In such an arrangement, defectors may be able to invade and capture cooperator-held areas, but then be driven to extinction because of the absence of cooperation; cooperators survive as fugitives by recolonizing those areas (58). Thus, tightening feedback loops through local interactions can enhance cooperation, and possibly coexistence.

However, tight feedback loops of this kind do not guarantee that cooperation will evolve; the end result, indeed, may be just the reverse. Spatial localization of interactions can also reward greed, selfish behavior, and spite. For example, trees evolve strategies to shade out neighbors (61), or to interfere with neighbors' roots, through mechanisms that would be too costly if their effects were diffused over large areas (62–64); indeed, it has been suggested that this can lead to a potential tragedy of the commons (63, 65). Similarly, plants and microbial organisms produce allelochemicals that poison neighbors (66), and selection for these traits depends critically on the fact that the allelochemicals will not be diffused over broad areas but will remain close enough to poison the most intense competitors.

The importance of this phenomenon was made clear in early experiments by Chao and Levin (67), who demonstrated that efforts to evolve the production of the anticompetitor toxin colicin in *Escherichia coli* failed in well-mixed environments, because cheater genotypes emerged that were resistant to the toxin but did not need to pay the metabolic cost of production of the toxin. In structured habitats, however, all three types could coexist, because of the localization of interactions. Incorporation of the three genotypes into an interacting particle model on a lattice demonstrated that coexistence would be possible, again through spatiotemporal oscillations (68). Experimental work confirming the results of this model completed the story, poetically describing it as “a real-life game of rock-paper-scissors” because of the nonhierarchical nature of the competition (colicin producer > wild type > cheater > colicin producer) (69).

The lessons from nature translate immediately into some lessons for understanding human social evolution. Appiah (70) discusses the hostility that is often evident between closely related peoples, in which groups need to self-identify and distinguish themselves from “the other.” Such groups are much less likely to engage in hostilities with peoples that are very different, and with whom they have not had a record of conflict over resources. What had its origins in real competition for resources has become translated into a pattern of antagonistic interactions, even when there is no longer reason for it. Here again, spatial localization has led both to cooperation (among individuals in the in-groups) and spite (between individuals of different, but closely related, groups).

The role of spitefulness in human societies has been the topic of several fascinating investigations (71–73). Without question, humans engage in spiteful behaviors for a complex of reasons, many likely owing to some vestigial selective benefits. The explanations, however, must continue to be speculative without a great deal more research.

Social Norms and Group Formation

It should be obvious from the discussions of the last section that issues of the maintenance of public goods rely heavily on population structure, and in particular on the formation of collectives that facilitate group decision-making and provide the benefits of a local commons. How then has evolution, genetic and cultural, shaped the formation of groups, and the emergence of more elaborate societies?

Coupled with these questions is the emergence of the social norms and customs—and ultimately, the laws, taxes, and incentives—that bind groups and societies together (74). It is the existence of groups that makes such instruments possible, and the existence of the instruments that makes groups possible; hence, one cannot really be considered without the other, and the focus should be on the coevolution of population structures and the rules that sustain them (75, 76). It has been pointed out to me that dominance hierarchies within populations may represent some of the earliest examples of norms.

The study of social norms has gained a great deal from the ability to perform experiments on group behavior, such as the work of Ernst Fehr and others (77–79). Through clever experiments, Fehr and collaborators demonstrate that individuals will pay a price to sustain a social norm that, for example, helps sustain a public good; they will punish others who violate the norm, at cost to themselves, and indeed, punishment itself becomes a norm that can evolve from repeated interactions. This punishment is the mutual coercion, mutually agreed upon that Hardin proposed (25), and that Ostrom and others have demonstrated for small societies (26).

Exemplary of this mutual coercion is how collectives of individuals extracting resources from a common pool might regulate use to avoid depletion, ostracizing individuals who overexploit the resource (80). As Tavoni et al. (80) show, maintenance of the norm in their model is possible only if the number of cooperators can be elevated above some threshold level; thus the model may exhibit multiple stationary states, a cooperative one in which the norm is enforced and a noncooperative one in which the resource collapses to much lower levels. A corollary of this result is that cooperation and the maintenance of a commons may be fragile, subject to collapse as external parameters vary (3, 81). The results also have an interesting parallel in the way international agreements are often structured, dependent on reaching a threshold level of signatories before they become activated (82).

In many natural situations, pattern has fundamental adaptive importance. Examples include the wing patterns on butterflies or similar templates for apostatic selection in other species, which, among other things, may make attractive search images for predators (83–87). Natural selection acts on the variation in color or other patterns, say in prey organisms, shaping the observed phenotypic and genotypic distributions, often through coevolution with other species groups (88). However, the initial reasons for the existence of the variation may have no adaptive explanation, and may represent no more than stochastic effects, or by-products of selection for other features.

Similar considerations apply to the formation of patterns in the distribution of individuals within populations. Random initial spatial (or other) distributions of individuals will necessarily result in some degree of clustering, providing a template for subsequent reinforcement (89), as well as for cooperation and resultant adaptive behaviors to evolve, as in the formation of slugs in the cellular slime mold (56), a collection of individual amoebae that provides collective benefits, on average, to the genotypes that make them up. Aggregation may increase relatedness, and relatedness may increase aggregation; but it may not make sense to ask, as for the chicken and the egg, which came first (see, e.g., refs. 53 and 90). Random initial associations may become reinforced by aggregation, in space, or in opinion,

possibly through simple attraction or imitation alone, followed by the stabilization of group boundaries through mechanisms that discourage intergroup interaction. Such devices will give groups integrities that make collective action and collective benefits possible, and make cultural group selection feasible (91, 92). The group's boundaries then can become reinforced, in concert with the emergence of customs, norms, and more formal structures like laws, institutions, religions, and societies (93).

Insurance, Prosociality, and Public Goods

John Nash showed that the only equilibrium in the prisoners' dilemma game was mutual defection (94, 95); still, clearly there are many ways in which individuals skirt the tragedy of the prisoners' dilemma, finding cooperative solutions that benefit all. An exciting new direction, involving mechanism design theory, helps in the understanding of when such cooperative solutions are possible in the presence of asymmetric information (96); but the simplest approaches assume perfect information about everyone's options. Under such circumstances, one can calculate the solutions that will yield maximum social benefit, and ask whether such solutions represent equilibria in a game-theoretic setting; if they do not, are there intermediate solutions that at least go part way? (A similar taxonomy is elegantly developed in chapter 2 of ref. 97, where the importance of the discount rate is also made clear.)

As a case in point, Avinash Dixit, Dan Rubenstein, and I examined the common practice in East Africa and elsewhere of herders who share grazing grounds as part of an insurance arrangement against the vagaries of weather and other conditions (98). In the two-player case, each herder invests an amount x (his private effort) in his own selfish interests (cattle), and an amount z (his public effort) in a public good (land quality). The total gross payoff (excluding investment costs) from having x cattle grazing on his land in a given year is given by a Cobb–Douglas production function

$$Ax^\alpha z^\beta,$$

where $A = A(t)$ represents the yield potential (which varies stochastically from year to year) in year t , and the exponents represent the output elasticities associated with private and public efforts, respectively. The player who gets a lower realization of A in 1 y can transfer part of his herd, just for that 1 y, to graze on the lands of the player with a higher realization of A . Given two players, with the potential for a transfer of m cattle, for example from habitat 2 to habitat 1, the total welfare is

$$W = A_1(x_1 + m)^\alpha z_1^\beta + A_2(x_2 - m)^\alpha z_2^\beta - (1/2)c(x_1 + z_1)^2 - (1/2)c(x_2 + z_2)^2,$$

where this function includes not only the payoffs in both habitats, but also the (quadratic) costs of investment. The exact forms of the functions—e.g., the quadratic cost functions—is not crucial for the results, but allows detailed computations for illustration.

It is straightforward (albeit laborious) to compute the maximum of W as a function of the inputs x_i , z_i , and m ; however, whether it will be self-sustaining in a repeated game (a subgame-perfect Nash equilibrium of the repeated game) will depend fundamentally on the discount rates the players use (we assume symmetry in this problem, for mathematical convenience; but there is no reason to assume that in reality). If the optimal solution is an equilibrium of the game, the problem is solved; if not, however, one can search for a second-best solution, a constrained optimum that allows the transfer of fewer cattle. The second-best solution is the allocation that maximizes total welfare subject to the equilibrium constraint. Finally, in work not yet published, we have demonstrated that prosociality, which is expected to be an important factor in these small societies with

high genetic and marital relatedness, improves the potential for maximizing total welfare. In this case, of course, the welfare function is modified to reflect the value that one places on the others' well-being.

In other unpublished work, Dixit and I have developed a more general framework, an extension of a one-group model already published by Dixit (99). In this framework, the individual utility of individual i in group g is given by

$$v_{gi} = y(x_{gi}, Z_g) - (c/2)(x_{gi} + z_{gi})^2 + \gamma_g \sum_{k \neq i} y(x_{gk}, Z_g),$$

in which Z_g represents the total public good, y is the yield, x_{gi} and z_{gi} are the private and public contributions of individual i in group g , the second term is the cost of investment, and the coefficient γ_g represents the prosociality the individual exhibits toward other members of her group. In this formulation, there is no prosociality toward individuals not in the group; but this assumption obviously can be easily relaxed. Also, prosociality here describes behaviors, not attitudes, and hence could be imposed or influenced by social norms, taxes or other incentives.

In the above, y again may take a Cobb–Douglas form, but we also consider alternatives. Finally, the total public good is given by the sum of the individual contributions within the group, plus some leakage from other groups (consider for example clean air within a community or nation, which will have indirect benefits to neighboring communities or nations.); again, other forms can easily be considered.

For the one-group model, Dixit previously derived the game-theoretic solution (99), in which each player maximizes her investments conditional on what the other's strategy is, and showed that for low prosociality, there is a tragedy of the commons; that is, there will be no contribution to the public good (the absence of temporal fluctuations in environmental conditions has removed the insurance benefits that make cooperation work for the herdsman). For sufficiently high prosociality, positive contributions to the public good emerge; and in the limit as prosociality tends to 1 (individuals value others as much as they do themselves), the solution tends to the collective optimum. In the more general formulation with multiple groups, we show that the public contribution may emerge locally in some groups, and that the leakage of benefits can then lead to global cooperation, depending on the topology of the interaction network. Beyond such simple arrangements, experiments such as those of Fehr, complemented with field studies like those for the ultimatum game (100), demonstrate that individuals indeed will pay a personal cost to sustain a social norm that ultimately contributes to the collective welfare (indeed, there are also countless examples, like foot-binding in China, where the sustained norms reduce total welfare, although they may maintain group cohesion). Such behaviors may seem to be irrational in the short term, violating a view of humans in terms of *Homo economicus* (101, 102); but they may arise because of the individual incorporation of heuristics, like fairness, that substitute for calculation in particular situations, essentially a consequence of bounded rationality (43). Understanding the factors that guide the adoption of such rules must embed individual realizations within a broader framework in which classes of similar games are considered, leading to the necessity of developing a theory of metagames (103).

Collective Phenomena and Collective Decision-Making

In the previous sections, I have argued that collective action can be effective if it includes enforcement, and that prosociality can be an important contributor to the maintenance of public goods and common-pool resources. Discounting, however, makes cooperation more difficult to sustain.

Hardin argued that the solutions to commons problems involve mutual coercion, mutually agreed upon, and studies of Fehr and others demonstrate the importance of social norms, a form of collective decision-making (25). Therefore, in this section, I turn to the last remaining theoretical puzzle, an understanding of how collective decisions are made, and the role of leaders and followers in attaining consensus. Of course, the theory of how societies vote and how they should vote has been a staple of economics and the decision sciences for many decades (104–107). In most situations, however, the way human groups arrive at collective decisions is much more bottom-up, based on a balance between innate tendencies and knowledge on the one hand, and imitation on the other. What then is the role of leadership? How is consensus achieved in democratic societies, and how important are those who are more likely to follow than lead?

These questions are at the core of collective decision-making, and naturally have been the focus of a rapidly expanding literature, from behavioral ecology to statistical physics (108–111). The evolutionary conundrum is a classical one in behavioral ecology, involving a “game” between producers (in this case, of knowledge) and scroungers (112). When should one be a producer and when a scrounger, and do successful foraging groups achieve a stable balance between them? Much of the early work on this problem considers this as an either/or decision (113), but in reality the tradeoffs are more nuanced. For example, Guttal and Couzin (114; see also ref. 115) assume that individuals have two evolvable parameters, representing investment in gradient-following and neighbor-following, and allow evolution to tune these parameters within a game-theoretic setting. Depending on conditions, the end result is often a bimodal population of relative leaders (gradient followers) and imitators (neighbor followers).

Couzin and coworkers (111, 116) explore theoretically and experimentally the potential for consensus in groups involving different mixes of leaders (with divergent goals) and imitators, and find that unopinionated (or perhaps just uninformed) individuals are crucial to the development of consensus, and to the nature of consensus. The first efforts in this vein focused on testing the hypothesis in mobile animal groups, using strongly schooling golden shiner fish, and more generally on the nature of consensus within animal populations searching for targets, but where there is no variability in terms of how strongly opinions are held (111, 117–119). A major conclusion is that, although leaders obviously are important, the unopinionated are also crucial to the consensus in their ability to connect the population, and to shift momentum from one direction to the other.

The assumption of no variation in strength of opinion can be relaxed experimentally, as well as theoretically, by training individuals to individual targets. The unopinionated then take on even greater importance, making it more difficult for strongly held minority opinions to dominate a population's consensus. In populations with small numbers of unopinionated individuals (followers), the consensus that is achieved may be dominated by a minority of individuals with strongly held opinions, who basically are able to overrule the more wishy-washy majority. As the number of unopinionated increases, at least up a point, it becomes harder and harder for the minority to prevail. For sufficiently large numbers of unopinionated, neither group really holds sway, and group directionality becomes largely random; but, before that point, the unopinionated shift the consensus to the majority opinion (110).

It is of course a big jump from golden shiners to humans, so more has to be done to justify conclusions about human decision-making. Ultimately, there is no substitute for empirical data; but appropriate models of decision-making can shed some light, and point the way to possible experiments. For example, Couzin et al. (110) adapt a (n adaptive network) model of Huepe et al. (120), considering a network of individuals with initial biases, who change their opinions based on their neighbors' opinions as well

as on their intrinsic biases; they also change their neighbors based on similarities of opinions (see, for comparison, ref. 121). A second investigation builds on a model of Peyton Young (122, 123), which considers the adoption of human conventions, like language or currency use. Again, individuals have a preferred state, but switch with a certain probability based on their interactions (there is no sense in carrying around dinars if nobody else will accept them); this has some similarities to the majority voter model (93, 124). The results of these more realistic models of human decision-making are strikingly similar, and provide evidence of how labile the electorate really is; this will not come as a surprise to political junkies, but it applies as well to the rapid population shifts from adoption of fads to attitudes about climate change and what must or must not be done about it (125, 126).

Concluding Thoughts: The Emergence of Societies as Complex Adaptive Systems

Managing public goods, and indeed any commons situation, raises challenges that have often been addressed via Darwinian mechanisms, involving the interplay of genetics and culture (127). In human societies, Hardin argued that success requires mutual coercion, mutually agreed upon; but where that has occurred and been effective, the coercion has generally been self-organizing, with agents grouping together, and reinforcing cooperation with norms, sanctions, and institutions (25, 26, 128).

Like smaller groups, societies from cities to nations are largely emergent phenomena, multicellular organisms that thrive on cooperation and differentiation of function. Planned economies, where an effort is made to control development from the top-down, in principle could regulate the number of doctors, bakers, teachers, and engineers, along with all of the other features that make societies function. However, top-down design lacks flexibility and adaptability (128) and suppresses initiative; the most robust societies are self-organized, dependent on individual incentives to ensure that there are enough of each profession and of each good and service. Governments are important, but at the margins, to create the infrastructure and incentives that are needed to address shortages. The study of cities and their growth is still in its infancy; but unsurprisingly it is thriving (129–131), and assuredly will grow in importance.

However, as we saw in the fiscal crisis of 2008, there are limits to what self-organization can accomplish. Adam Smith, father of the “invisible hand,” is often cited by neoclassical economists as arguing for *laissez-faire* because, he wrote, of the individual in society, “By pursuing his own interest, he frequently promotes that of the society more effectually than when he really intends to promote it. I have never known much good done by those who affected to trade for the public good” (132). However, Smith also warned about the potential for businesses to collude against the public, recognizing that markets could not be entirely without regulation, because industry’s objectives “in any particular branch of

trade or manufactures, is always in some respects different from, and even opposite to, that of the public” (132). There is, however, nothing anti-Darwinian in the notion that societies must restrain the process of competition and selection among its members; higher-level cultural selection has always been part of the history of the biota. Ultimately, for societies to flourish, they must rely on the integration of bottom-up mechanisms—including competition, prosociality, and collective action—with top-down mechanisms involving norms, rules, rewards, and punishment to achieve equitable, robust, and adaptive governance.

Mutual coercion, mutually agreed upon, has been successful over and over again in small societies. Arrangements such as the lobster gangs of Maine, the water temples of Bali, and the Tribunal de las Aguas de Valencia, all give evidence that self-organized solutions, with emergent norms, can help protect public goods, combining top-down and bottom-up mechanisms. As we move to larger scales, however, for example in protecting climate or biodiversity as public goods, the challenges become greater (3). Recent work demonstrates the importance of great inequities in wealth, and of heterogeneity more generally in addressing global problems (133). These issues of scale and heterogeneity led the late Ostrom to argue for a modular, polycentric approach to addressing climate change (27), which means starting locally, and building up from there. And I would argue that it also means agreements between subsets of nations, as building blocks for larger-scale agreements; indeed, from what we know about Darwinian selection and the evolution of multicellularity, in which modules can become building blocks for emergent complexity, this seems the most hopeful approach to global sustainability.

The greatest challenges to achieving a sustainable future in an increasingly interconnected world rest in finding solutions to dealing with public goods and common-pool resources, especially when the individual agents are nations or distributed networks of individuals. The lessons to be derived from evolution and evolutionary theory are a starting point, but scaling up to larger and larger groups, in a technological world in which individuals can make sophisticated calculations about their futures and their interests, create novel challenges, both from the viewpoints of applications and mathematical theory. Addressing such challenges is essential if we are to address our own futures, and represent some of the most exciting challenges for sustainability science.

ACKNOWLEDGMENTS. I thank Iain Couzin, Partha Dasgupta, Avinash Dixit, Paul Ehrlich, Carole Levin, Jacob Levin, Carey Nadell, Jorge Pacheco, Dan Rubenstein, Donald Saari, Corina Tarnita, and two anonymous referees for careful reading and helpful comments. I thank my colleague and former student, Adi Livnat, for illuminating discussions on hyperbolic discounting, and Paul Ehrlich for his observations on hierarchies. Financial support was provided by National Science Foundation Grants EF-1137894 and GEO-1211972, and John Templeton Foundation Grant QEB RFP-12-14 through the National Philanthropic Trust.

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