

Enough of the “selfish gene,” already. It was a clever mental exercise once. But the anthropomorphism has also been grossly misleading. Even Richard Dawkins now seems to acknowledge as much (2006). The phrase fundamentally confuses levels in biology. It implies that genes can have intent and moral perspective (de Waal, 2009: pp. 38–45). The notion emerged just as sociobiology began promoting the genetics of behavior, and it was all too easy to consider all behavior “selfish.” Explanations of cooperation, “altruism,” and eusociality were reduced to genes through the concepts of inclusive fitness and kin selection. The supremacy of the individual seemed to epitomize Darwinism. These concepts thus gradually became entrenched, and now appear in virtually every textbook: another sacred bovine?

Recently, however, E. O. Wilson, the prominent founder and advocate of sociobiology, has renounced kin selection in explaining societies with a single reproductive individual (Nowak et al., 2010). Three decades of research have shown that many cooperative-breeding societies (such as termites) do not exhibit the required haplo-diploid genetic structure. Moreover, many species that do (including sawflies and hornails) are not social. The documented cases and the explanation do not align. Rather, the societies – from ants and honeybees to beetles, shrimp, and naked mole rats – all seem to have nests with restricted access, guarded by just a few individuals. The social cooperation seems just an “ordinary” adaptation to certain conditions. The striking reproductive structure, Wilson now contends, is an evolutionary consequence – not a cause – of the social organization.

Wilson’s dramatic turnabout illustrates a wider shift in perspectives about how cooperation evolves (Brosnan & Bshary, 2010). For decades William Hamilton’s (1964) notion of kin selection has largely eclipsed Robert Trivers’ (1971) concept of reciprocity. While the former is ubiquitous in introductory textbooks, the latter is nearly always absent (Allchin, 2009). But the once popular reductionism is now yielding to social and cultural evolutionary approaches. In case after case, reciprocal interactions – immediate or deferred, direct or indirect, and mediated by rewards, sanctions, or reputation – are emerging as significant. As Wilson’s claims suggest, higher levels of organization can govern the genetics. The “selfish” gene has been *domesticated*. Here, then (in the spirit of this issue’s special theme), I describe some recent research on the evolution of cooperation. (For a textbook-style summary of earlier studies, along with classroom visuals, see <http://evolutionofmorality.net>.)

○ When Non-Kin Cooperate

The explanatory limits of kin selection are plainly evident where non-kin cooperate. For example, consider the case of two unrelated capuchin monkeys, Sammy and Bias (described by primatologist Frans de Waal in his recent book, *The Age of Empathy*, 2009: p. 171). They had learned to jointly pull a spring-loaded tray to obtain food: a simple form of cooperation. On one occasion, however, Bias did not get her share before the

tray snapped back out of reach. She threw a tantrum. Sammy finally returned to the task and Bias, too, got her reward. Both clearly understood the implicit contract of mutual effort. *Quid pro quo*. Following Trivers’ model, their help was based on reciprocity. In the same way, de Waal observes, unrelated chimps will share meat after a hunt. Often, they repay social favors. Indeed, in sustained observations of a captive chimp troop, the exchange of grooming and special food items tended to even out in the long run (de Waal, 1989). Sharing was not based on kinship. But neither was it blind.

Recently, Cambridge zoologist Tim Clutton-Brock (2009) reviewed the growing list of cases of cooperation between non-kin in animal societies (also see Dugatkin, 1997). For example, stickleback fish share risk in approaching predators (such as trout) to assess the degree of threat. Olive baboons assist each other in mating competition. Ungulates exchange grooming. Rats not only cooperate, but their tendency to do so grows with experience. One can add all sorts of cases of cooperative predation (such as among pelicans), as well as defense against predators (such as mobbing by meerkats). In such cases, the mutual benefits are immediate. The consequences for natural selection are easy to imagine. They echo the interspecific mutualisms familiar from textbooks. But these should be distinguished, Clutton-Brock cautions, from occasions where the benefits are deferred – more problematic in an evolutionary context.

The hitch is that helping behavior may never be reciprocated. Delay opens the way to free-riders: organisms that harvest the benefits while contributing nothing. Reciprocity, when deferred, requires trust or long-term accounting. The problem of lag time was investigated with blue jays by David Stephens and colleagues at the University of Minnesota (Stephens et al., 2002). They examined successive rounds of potentially cooperative interactions, but added a key feature: delaying the pay-offs. The birds could assess each other’s behavior after each step. The delay allowed trust to develop before sealing the “deal.” Blue jays will extend cooperation and achieve greater rewards, they found, when the “temporal discounting” is reduced. Kinship aside, cooperation can occur through reciprocity when trust can be established (or enforced – see below).

The kin-selection bandwagon was thus premature. For example, Florida scrub jays stay at home and help raise their siblings – even when they are reproductively mature. That was quickly labeled an example of inclusive fitness. However, Glen Woolfenden and John Fitzpatrick (1978) showed how this was a social adaptation. Males secure better territory: they help enlarge dad’s range and then cleave off their own. Females, by “sitting and waiting,” secure better mates. Individual reproductive strategies, not kinship, shape cooperative behavior in scrub jays.

Accordingly, one must reconsider the role of kin selection, even where organisms are related. Indeed, mathematically, the conditions for kin selection prove quite narrow: only when selection is weak and fitness effects are strictly additive. For example, selection cannot be

frequency-dependent. Yet when cooperators become more common, cheaters benefit more. Also, fitness depends on the whole community, not just immediate neighbors. One research team has developed a more general form of Hamilton's original formula, but the revised calculation adds new variables for population structure. In the cases they studied – microbes – these populational factors were far more significant than relatedness (Smith, et al., 2010).

E. O. Wilson bolstered his recent criticism of kin selection with similar mathematical analyses (Nowak et al., 2010). He and his colleagues also emphasized the unrealistic requirement for direct one-on-one interactions. Nature is more complex, they claim. Ultimately, kin selection may be relatively rare. Inclusive fitness, important in interpreting sex ratios and certain reproductive tradeoffs, seems limited in explaining cooperation and sociality.

○ When Society Regulates Individuals

Because delayed reciprocity is susceptible to cheaters, cooperation cannot evolve if they proliferate. But solutions may emerge through social interactions and individual choice (not at the genetic level). For example, de Waal modeled the basic dilemma for his capuchins. After the monkeys had learned a basic cooperative drill, he restricted the food reward to only one individual. The privileged monkey (playfully dubbed “the CEO”) usually shared the prize. When he did not, however, on subsequent trials the would-be cooperator went “on strike” (de Waal, 2009: p. 176). Here, failure to share was kept in check. “Opting out” was a modest, local form of social accountability.

The same pattern is reflected in the widely known case of vampire bats (Wilkinson, 1990). The bats share blood, accommodating the risk of not feeding on any particular night. But repeat beggars are denied help if they have not reciprocated. One might say that cooperative behavior is enforced by a form of peer pressure (an analogy not lost on young adults!). Darwin expressed it a bit more eloquently, of course: humans, he wrote, tend to be “greatly influenced by the wishes, approbation, and blame of [their] fellow-men” (1871: p. 86). Either way, negative social consequences seem to shape individual behavior.

Yet sanctions are costly. Are such costs sustainable? In many mathematical models, a system in which noncooperators are punished seems stable, once established. However, individual punishers cannot necessarily gain a foothold. How can such a system originate? In a recent model, Boyd et al. (2010) introduced *coordination* of punishment. The ability to gang up on free-riders proved critical in initiating cooperative groups. That finding seemed to resonate with earlier anthropological claims that such coordination helped early humans to level primate hierarchies, yielding egalitarian societies (Boehm, 1999). Newly emerged language may have facilitated that coordination (Melis & Semmann, 2010). Another possible mechanism, demonstrated in other models, is allowing individuals to choose their group (punishing vs. unregulated; Hauert et al., 2007). Both yield a social system of cooperation enforced through punishment.

One need not limit effective interactions to punishment, however. Rewards also work. Indeed, in one study of almost 200 human subjects, rewards became more common as the group interacted (while punishment waned). The outcome was higher levels of sharing (Rand et al., 2009). Incentives can be as effective as sanctions.

Another study considered the relative roles of rewards and sanctions (Ule et al., 2009). Participants were sorted into short-term pairs in successive rounds. One Donor could either give or withhold donations, or impose costs on the Recipient, on the basis of information about the Recipient's own recent behavior as a Donor. But there was no symmetrical interaction. Enforcement of direct reciprocity was not possible. All effects were indirect. Ultimately, generous givers fared better than free-riders. In the long run, punishment was minimal. Still, when compared with the behavior of a control group, punishment critically kept

free-riding in check. Incentives and sanctions in tandem helped generate a system of indirect, or network, reciprocity. That could explain why even in a large society, persons might incur costs to reward strangers they may never meet again.

The gamut of mathematical models and experimental games by economists, psychologists, and evolutionary biologists is nicely summarized by Karl Sigmund in *The Calculus of Selfishness* (2010). Even adopting self-interest as a guiding motivation, many social conditions predictably yield cooperation. Direct reciprocity underscores the role of repeated encounters; indirect reciprocity, the role of reputation. Incentives can foster fairness and trust. Free choice and enforcement enable joint efforts and public goods. Ultimately, the social trumps the individual. The higher level of organization develops its own distinctive properties. Cooperation is *emergent*. Such emergent properties sharply curtail the explanatory power of genetic reductionism, inherent in the notion of the “selfish gene.”

But how realistic are such models? Do humans behave according to their assumptions? A team of 14 anthropologists investigated the willingness of individuals to punish noncooperators – at a cost to themselves (Heinrich et al., 2006). Unlike earlier studies, they documented this tendency across an impressive diversity of 15 cultures: from Pacific islanders and African pastoralists to Siberian hunters and U.S. college students. Furthermore, the degree of endorsed punishment covaried with a measure of the culture's generosity (a conclusion echoed in another study of 16 diverse groups in 6 developed cultures; Gächter et al., 2010). Cooperation was correlated with readiness to punish.

A more recent follow-up study addressed how the cultures varied in their specific conceptions of fairness: just *how much* were others expected to share? (Heinrich et al., 2010). Two variables were confirmed. First, people tend to share more (that is, give closer to one-half to another person) when their culture depends more on economic markets. Apparently, societies that rely on the exchange of goods and services deem equitable transactions important, and thus support a norm of fairness. Second, the willingness to punish increases with population size. As populations become larger, ephemeral interactions with strangers increase. Without direct reciprocity, however, the need for unmediated trust is sharpened. For the researchers, these findings helped underscore the role of social institutions and norms – not innate tendencies based on kinship – in establishing cooperation in large societies. Once again, emergence at the social level is key. Cultures can evolve on their own and govern individual behavior.

○ When the Social Environment Selects

Another important thread of research has focused on moral feelings – what Darwin and his peers called the moral sentiments. What is the origin of the impulse to help victims of a flood or earthquake in some remote region of the globe? Or help strangers when a skyscraper bursts into flame? Certainly not calculations of kinship. Nor anticipations of reciprocity. Psychological and evolutionary contexts (proximal and ultimate) are distinct (Sober & Wilson, 1998). An individual's motivational system is autonomous, even if shaped by natural selection.

Empathy may possibly be learned through enculturation or explicit education – another form of social-level regulation. Yet even young children may express it spontaneously. For example, they often console others who are crying. Felix Warneken and Michael Tomasello (2006), at the Max Planck Institute for Evolutionary Anthropology in Germany, documented how infants 18 months old provided help to adults when they noticed simple problems as the latter completed some task. Chimps do the same, although at a later age. Chimps have also responded with concern to the mock-crying of their human caretakers (for example, Washoe, responding to Beatrix Gardener in the 1960s; or Yoni, responding to Nadia Ladygina-Kohts in the 1930s). De Waal (1996, 2009; de Waal & Suchak, 2010) catalogues numerous other examples of

empathy among primates, showing the ancestral roots of such responses: chimps venturing into water to save others (and often drowning themselves); chimps assisting an older colony member with arthritis; snow monkeys tolerating a troop member born without hands; macaques offering consolation after a sexual assault; and so on. De Waal (2006) justly criticizes the “veneer theory” of human morality: the view that we are selfish to the core, with only a thin surface of morality imposed by society. Some empathetic motivations seem innate.

How could moral instincts evolve, if not by kin selection? Darwin provided a model of sorts in his concept of sexual selection (1871). Organisms adapt, but *to other organisms*: namely, to a social environment. Such selection has generated some pretty remarkable traits in reproductive contexts: peacock plumage, Irish elk horns, whale songs. So, too, for ancestral human societies? Behavioral traits that enhance personal survival in a social world will (when genetic) contribute more genes to succeeding generations. Such a mechanism is now invoked to explain the origin of several human social traits: language skills, “mirror neurons” (that enable us to interpret each other’s perspective), and “social intelligence” (such as the ability to detect liars) (Gazzaniga, 2008). For de Waal (1996, 2009), our primate ancestors also evolved other innate social tendencies that we inherited: emotional contagion, concern for others, and conflict resolution. To the degree that we are social animals, we should expect moral sentiments and cooperative tendencies to be integral to our evolved heritage. The social environment can be a selective force just as much as the physical environment.

Darwin’s concept of artificial selection also seems relevant. As a gentleman farmer Darwin readily perceived how domesticated animals exhibit traits that differ from those of their wild cousins. That results from generations of intentional selective breeding. Accordingly, one might say that humans have also been “domesticated”: by each other. Society will collectively “breed” for innate cooperative and social dispositions. The irony is that humans themselves create their own social environment.

○ Domesticating the “Selfish Gene”

In retrospect, the concept of the “selfish gene,” like Robert Ardrey’s “territorial imperative,” seems like a nightmarish expression of individualism drawn from Cold War politics and capitalist economics. While it inspired much thinking (some of it fruitful), it also seemed to biologize society. It gave nature-based justification to ideological views (Lewontin, 1996; Rose, 1997). The authority of science appeared to endorse (inappropriately) certain cultural values. “Selfishness” was *naturalized* (*Sacred Bovines*, August 2006, February 2008). Genuine cooperation became an aberration, or a lie, or at least an explanatory paradox. The recent wave of research highlighting the role of emergent properties now makes quite clear those earlier biases and distorted assumptions.

Of course, one may be equally blinkered by overly romantic views. Humans are hardly universally moral or beneficent. (Witness the atrocities at Abu Ghraib prison or in Bosnia, Rwanda, and Darfur, or even the harassment of gays and others in school settings.) Researchers have not neglected this darker side of behavior, either. For example, Keith Jensen (2010) has explored the conditions for spite and runaway punishment. Consider the role of oxytocin, a peptide neurotransmitter-hormone released from the hypothalamus. In recent years it has been shown to regulate mother–infant bonding in sheep and rodents, pair bonding in voles, and group size in zebra fish (Miller, 2010). In humans, it seems to promote empathy, trust, and generosity, while diminishing unfair exploitation. One might thus want to champion a new biological basis of – and physiological mechanism for – cooperation. Indeed, practical applications of oxytocin as a “social lubricant” are already underway, from business to personal romance to law enforcement. However, according to a Dutch study published last June, those rosy effects do not seem divorced from antagonism toward outsiders (De Dreu et al., 2010). Here, in-group loyalty seems coupled to out-group aggression. Oxytocin’s regulatory

role apparently has two social edges: fostering both parochial helping and intergroup conflict. Meanwhile, analysis of anthropological data has indicated that such conflicts – between competing hunter-gatherer groups – could well have been significant in human evolution (Bowles, 2009). Well (no surprise perhaps), biology is complex. One extreme view will not be solved by an alternative extreme.

As research continues, knowledge grows, yes. But sometimes, concepts can change dramatically. The overall gestalt can switch. Paradigms can shift (Kuhn, 1970). Sacred bovines can topple. Genocentric views of cooperation now seem quite limited. Instead, genes, minds, and society interact, integrating different levels. In particular, higher levels of organization can govern lower levels. The once faddish “selfish gene” has become domesticated.

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