

mechanistic work on the response threshold concept, I think this part of the book reviews important work in social insect biology and in behavioral genetics in general.

Page finishes his book by focusing on the reproductive ground plan work he has conducted in recent years with Gro Amdam and others. This is the study of how core genetic modules (primarily relating to reproductive physiology) have been reshaped by selection for eusociality. The idea was originally proposed by West-Eberhard for social insects, and has strong overlap with evo-devo ideas in general. Page also touches on work conducted with Timothy Linksvayer and others on indirect genetic effects on social behavior. This work explores how genes expressed in relatives (parent/offspring/siblings) interact with genes expressed in individuals to shape phenotypes that occur at both the individual and colony levels. Both of these research agendas are ongoing and are at the vanguard of research into social evolution. Page does a good job of reviewing the work done in his lab.

In summary, when studying a complex system it is often useful to take careful stock of where we are versus how far we have to go. In studies of vertebrate brains, for example, this is inescapable since our understanding of these systems pales in comparison to their complexity. It is entirely possible to learn massive amounts about the behavior of individual neurons without understanding how the neurons function as a group when linked together into large circuits. In the study of simpler, yet still profoundly complex systems, such as honey bee colonies, similar themes are present. Even though I do not think Page has captured the “spirit of the hive” in his book, I do think he has reviewed careful and important work on honey bee physiology and genetics, and I think that this review will ultimately enrich our understanding of these societies at every level of biological organization.

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Quick guide

Reciprocal altruism

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What is reciprocal altruism? In 1971, Robert Trivers coined the term ‘reciprocal altruism’ to describe a process that favors costly cooperation among reciprocating partners. In principle, altruism confounds the basic logic of evolution by natural selection because individuals incur fitness costs while providing benefits to others. Altruistic traits can evolve only when some cue allows altruists to direct benefits selectively to other altruists, and thereby increase the relative fitness of altruists. Three types of cues provide a basis for such assortment: recent common descent, proximity in viscous populations, and previous behavior. The first two types of cues are the foundation of kin selection, and the last cue is the basis of reciprocal altruism. The past behavior of other individuals provides a cue about whether they may carry genetic alleles that lead to altruistic behavior. Altruism can be favored if recipients restrict help to those from whom they receive help —I’ll scratch your back if (and only if) you’ll scratch mine.

Could you give some examples?

Textbook examples of reciprocal altruism include male baboons forming coalitions to gain access to sexually receptive females that are being mate-guarded by high ranking males. Craig Packer found that males most often supported the males from whom they received the most support. Gerald Wilkinson reported that when vampire bats return to their roosts after successful foraging trips, they sometimes regurgitate food for hungry nestmates. Wilkinson found food sharing was most often directed to kin and those that also shared food with the donor. Other well-known examples include egg trading by simultaneous hermaphroditic fish, predator inspection by schooling fish and the exchange of grooming in kind or for agonistic support in Old World monkeys and apes (**Figure 1**).

So, all questions answered then?
Not at all. Over the last few years, all

these examples have been disputed and alternative explanations have been proposed. For example, male baboons may form coalitions simply because it is the best strategy for each of them. Alone, neither may have much chance of taking a female away from a high ranking male, but together each has much better odds of taking control of the female. Vampire bats may share blood because they are persistently harassed by other group members, making it more costly to hoard food than to share it. Tim Clutton-Brock has played a prominent role in raising questions about the validity of explanations based on reciprocal altruism. As one after another of the ‘classic’ examples of reciprocal altruism was reinterpreted, skepticism about explanations based on this process has increased. If you took a poll of behavioral ecologists today, I think the consensus would be that reciprocal altruism is extremely rare, perhaps limited to a few large-brained species, such as primates or cetaceans.

Is it possible we’re confusing absence of evidence with evidence of absence? Maybe. As skepticism about explanations based on reciprocal altruism has increased, the standards of evidence for inferring direct reciprocity have become more rigorous. With this, there is now some risk of rejecting genuine examples of reciprocity because they do not meet the full burden of proof. The primate literature presents a good example of this problem. Across a wide range of species, we find positive correlations between the benefits given and received within pairs of individuals. For examples, female baboons spend the most time grooming females from whom they receive the most grooming, and this pattern is not restricted to close kin. We also find positive correlations between grooming given and coalitionary support received. These are the kinds of patterns we would expect reciprocal altruism to generate. However, correlational data do not provide evidence of contingency, that one individual’s behavior was dependent on the previous behavior of its partner, a critical condition for strategies based on reciprocal altruism. Moreover, we are unable to measure the benefits and costs associated with



Figure 1. Reciprocal grooming.

One adult male chimpanzee grooms another adult male in the Gombe National Park, Tanzania. Male chimpanzees cooperate with one another in a wide range of contexts and form close bonds with both close kin and unrelated males. (Photo by J.B. Silk.)

grooming and coalitional support. Thus, some dismiss the correlational evidence as inconclusive and favor simpler explanations, while others consider the correlations to be suggestive evidence of strategies based on reciprocal altruism. It is also important to remember that the existence of alternative explanations does not necessarily mean that they are correct. Wilkinson's original hypothesis that vampire bats selectively transfer blood to reciprocating partners was criticized, in part, because he did not provide convincing evidence of contingent sharing among non-kin. However, a recent set of experiments conducted by Wilkinson and Gerald Carter shows that the best predictor of food donations by one bat to another is the amount of food previously obtained from the same individual, not kinship.

Why isn't reciprocal altruism more common? Even if all of the putative examples of reciprocity were verified and accepted, it would probably still be true that reciprocity is much less common in other vertebrates than it is in humans. This is puzzling because there seem to be obvious benefits to developing long-term cooperative relationships with

other group members. Think of the efficiency that human societies derive from division of labor and exchange systems. It is possible that cognitive limitations, including memory capacity and processing power, might constrain the capacity for contingent reciprocity. Reciprocal altruism requires individuals to track their previous interactions with others in some way. They must also convert behavioral acts, such as being groomed or allowing a partner to share a food patch, into a common currency. Psychological biases that influence motivation and behavior may also inhibit the development of reciprocity. For example, preferences for immediate rewards over future rewards may create a strong temptation to defect on partners and jeopardize long-term cooperative relationships. Some find these arguments unconvincing because animals perform other kinds of tasks with apparently similar levels of difficulty. For example, macaques, hyenas, and piñon jays keep track of dominance relationships between other group members. Caching birds remember the locations of hundreds of food items, and can overcome the temptation to consume food items immediately.

But aren't humans 'special'?

Another possible explanation indeed focuses on special human traits, such as language. Tim Clutton-Brock has suggested that reciprocal reciprocity is easier to sustain in human groups because humans are able to inform their partners about their intentions and expectations and coordinate exchanges more effectively. Language may permit people to overcome the problems created by errors of perception (i.e. failing to realize that the partner had tried to help) or implementation (i.e. unsuccessful efforts to provide help). In a forthcoming paper, Sarah Mathew and her colleagues hypothesize that norms about cooperation, third-party monitoring and adjudication of pair-wise interactions and conflicts, and sanctioning of defection and cheating may also play an important role in stabilizing direct reciprocity in human societies.

What's the bottom line? It's wise to be cautious about invoking reciprocal altruism as an explanation for cooperative behavior in nonhuman species, but premature to abandon the possibility that reciprocal altruism underlies certain kinds of cooperative relationships. It would be profitable to assess the factors that stabilize reciprocity in human societies, because this information will influence estimates of the plausibility that strategies based on reciprocal altruism will exist in other species.

Where can I find out more?

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