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51 A Cognitive Approach to the Study of Animal Cooperation

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The study of cooperative behavior in animals has played a central role in the field of behavioral ecology (Dugatkin 1997). Moving away from early views that cooperation either permeated the animal world (Kropotkin 1908) or was completely lacking in nonhumans (Huxley 1888), modern behavioral ecologists are attempting to build a sound theoretical framework for understanding the evolution of cooperation (Hamilton 1964; E. O. Wilson 1975; Axelrod and Hamilton 1981; Brown 1983; Dugatkin 1997; Sober and Wilson 1998). Progress in building such models has been good, and this is reflected in the hundreds of controlled studies of cooperation in animals that can be found in the primary literature (Dugatkin 1997).

In the past, one of us (L.A.D.) has argued that there are four paths to cooperation (Dugatkin et al. 1992; Mesterton-Gibbons and Dugatkin 1992; Dugatkin 1997). These paths can go by slightly different names, but are generally referred to as reciprocity, by-product mutualism, group selection, and kin selection (Mesterton-Gibbons and Dugatkin 1992; Dugatkin et al. 1992). As with any attempt to build an umbrella theory, objections to slicing the cooperation pie into four pieces certainly exist.

Here our goal is not to settle these arguments, but rather to present the case that splitting cooperation into the four paths mentioned here is quite useful in terms of understanding the different cognitive prerequisites for various forms of cooperation to take place in animals. To accomplish this goal, we outline each of these four paths to cooperation; at the same time we describe what each path requires and how they differ in terms of recognition of individuals and memory of specific events (the two cognitive variables we focus on).

Before proceeding any further, it might be useful to briefly touch on the relationship between recognition of individuals and memory of specific events. One important facet of this relationship is that recognition of individuals can exist in the absence of memory of specific events, and vice versa. For example, I may recognize you by some mosaic of facial features, but not necessarily remember anything about what you have done. Conversely, I may be able to remember that someone did *X* to me, without recalling who it was who actually undertook *X*.

The notion of recognition of individuals itself is not without problems. It could be argued that it is simply one case of what might be thought of as "category" recognition (Barnard and Burk 1979; Dugatkin and Sih 1995, 1998). A great deal of empirical work in animals has shown that animals can distinguish things based on size (e.g., large versus small), color (e.g., red versus blue), etc. If animals are able to apply enough of these categories to other individuals, eventually individual recognition will come about (Barnard and Burk 1979). As we will soon see, some paths to cooperation require a simple form of category recognition, while others require recognition of individuals per se.

Reciprocity

Trivers (1971) suggested that one path to cooperative behavior among humans and nonhumans alike is reciprocity. Under Trivers's formulation, reciprocity evolves when the (potentially) minor cost that one individual pays to help another individual in need is repaid when the recipient returns the favor (reciprocated) some time in the future. Such a system, however, is subject to cheating (= not cooperating = defecting) because the greatest "payoff" attainable in such scenarios goes to the recipient of a cooperative action, who then can fail to reciprocate in turn.

To formalize the evolution of reciprocity, behavioral ecologists employ the prisoner's di-

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lemma game (Axelrod 1984; Dugatkin and Reeve 1998). Using mathematical formulas and computer simulations, Axelrod and Hamilton (1981) examined the success of an array of strategies (behavioral rules) in the iterated prisoner's dilemma game. They found that if the probability of meeting a given partner in the future was above some critical threshold, then a strategy called "tit for tat" (TFT; first created by Anatol Rapport) was a robust solution to the iterated prisoner's dilemma. TFT instructs a player to cooperate on the initial encounter with a partner and to subsequently copy the partner's last move. As such, TFT initially cooperates and then defects on defectors and cooperates with cooperators.

From a cognitive perspective what does TFT require in terms of recognition of individuals and memory? The answer, not surprisingly, depends on the ecology and population biology of the animal group being studied. In relatively rare circumstances, individuals involved in some sort of reciprocal interaction will have the same partner for all such actions. This might be due to individuals being somehow physically linked. Another scenario that might produce life-long partners is a scarcity of potential partners. Here partners are not physically bound together, but the lack of potential new partners in effect creates long-term interaction. When interactants are trapped with a given partner, all that is required to play TFT is the memory of a specific event (cooperation or cheating). Recognition of an individual, or for that matter recognition of any category, is not required.

A more realistic scenario for TFT involves individuals who are free to change partners and do so readily (Dugatkin 1997). In this case, TFT requires individuals to remember specific events (cooperation or cheating) and to recognize individuals. To play TFT when partners are swapped, you must do what your partner did on the last move, and that means an individual must recognize who they are paired with at any given moment.

While it may come as no surprise that primates possess the cognitive prerequisites to play TFT in such scenarios (see de Waal 1996), it is important to note that "simpler" animals such as guppies and even aquatic polychaete worms seem capable of playing TFT when trapped in a prisoner's dilemma (Sella 1985, 1988; see Dugatkin 1997 for a review). For example, *Ophryotrocha diadema* is a hermaphroditic worm that appears to engage in the "egg swapping" that is seen in many deep-sea fish (Fischer 1988). Individual worms pair up and take turns contributing eggs and sperm to matings. It is not known how these worms keep track of one another's behavior, yet "cheating" (failing to provide eggs at the appropriate turn) is rare comprising approximately 8 percent of interactions. (Sella and Lorenzi 2000). In fact, most of the time it is the availability of a new potential mate with riper eggs, and not cheating by one's partner that causes the dissolution of polychaete pairings. The fact that worms are capable of such behavior suggests that reciprocity and partner fidelity may be rooted deep in evolutionary time.

Kin Selection

Perhaps the most well-known path to cooperation is kin selection. Both Darwin (1859) and Haldane (1932) recognized that individuals were more prone to cooperate with relatives, but this idea was not formalized until the late W. D. Hamilton came up with his inclusive fitness or kin-selection models (Hamilton 1964). The heart of inclusive fitness models is that they modify prior formulations by considering the effect of a gene, not only on the individual that bears it, but on others as well; most important, those sharing genes that are identical by descent. "Hamilton's rule" (i.e., $rb\text{-}c > 0$) states that cooperation should be more common among kin because by helping kin, individuals are helping copies of their own genes, which just happen to reside in their blood relatives.

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What recognition and memory requirements must be met for kin-selected cooperation to evolve? Again, the answer depends on the demography and biology of the population under study. At one extreme, individuals may find themselves always interacting with kin and only kin during some stage of their lives. During that time, a rule such as "treat everyone as if they were kin" would be favored, and this would in turn remove any memory or individual recognition requirements from kin-selected cooperation. While this sort of rule of thumb generally works, it is susceptible to parasitization. For example, cowbirds parasitize other species of birds by laying their eggs in their nests (Ortega 1998). The victims of such duplicity almost always treat cowbird young as their own, doling out all sorts of parental attention. The parents in such nests have adopted the "if it is in my nest treat it as offspring" rule, which generally works but is susceptible to cowbirdlike cheating.

In most cases of kin-related cooperation, individuals encounter both kin and non-kin on a normal basis. In such scenarios, individuals only need to be able to distinguish kin from non-kin (Reeve 1989). While there is some debate about exactly how animals actually recognize kin (Grafen 1990; Brown and Eklund 1994), such discriminatory abilities have been demonstrated many times (Fletcher and Michener 1987; Hepper 1991; Crozier and Pamilo 1996; Holmes and Matio 1998). For kin selection when individuals encounter both kin and non-kin alike, categorical recognition is needed, but neither recognition of individuals nor memory is required. One way to see this is to recognize that while kinship is an important variable in animal social interactions, animals typically do not use conditional strategic rules like "Do *x* when someone does *y*; otherwise do *z*" (rules that require memory and recognition of individuals) when interacting with relatives. The more common rule of thumb in kin-selected cooperation is if that you are detected as a relative, you are treated one way; if not, you are treated another way.

Group Selection

Group selection has a long and controversial history within evolutionary biology (D. S. Wilson 1983; D. S. Wilson and Sober 1994; Sober and Wilson 1998). Here we focus on "modern" group selection or what is often referred to as trait-group selection. In trait-group models, natural selection operates at two levels—within groups and between groups. Within groups, cooperators are always at a disadvantage because they pay a cost that cheaters do not. However, it is possible that the productivity of groups may be positively related to the number of cooperators (the between-group component of trait-group selection). In these models, cooperation evolves if the within-group cost incurred is offset by some between-group benefit, so that cooperative groups are more productive than selfish groups (D. S. Wilson 1980; Sober and Wilson 1998). For such group-level benefits to be manifest, groups must differ in the frequency of cooperators within them, and must be able to "export" the productivity associated with cooperation.

At the most basic level, group-selected cooperation requires neither recognition nor memory. For example, it can be shown that some forms of cooperation can evolve by group selection if groups are formed randomly and individuals have no memory or recognition abilities (D. S. Wilson 1980). That being said, group-selected cooperation would be favored if cooperators were able to identify and interact with other cooperators (Eshel and Cavalli-Sforza 1982; Peck 1993; D. S. Wilson and Dugatkin 1997; Roberts and Sherratt 1998). This would require cooperators to categorize others as "cooperator" or "cheater," but they would not necessarily possess the ability to recognize individual (such abilities, however, would facilitate the evolution of cooperation to an even greater extent). In-group biasing, in which individuals show a strong tendency to favor those in their group, is one possible outgrowth of group-selected cooperation

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when categorization ("same group," "different group") is possible. To see how powerful in-group biasing can be, consider two examples—one from chimps and one from humans.

Warfare is often defined as large-scale, open hostility between groups, in which both sides in the conflict use lethal force against the other (Boehm 1992). According to this definition, chimpanzees do not engage in war, but between-group interactions in chimpanzees do resemble the raiding behavior so common among many tribes of humans (Boehm 1992, 1999; Wrangham 1999). During raids, all-male chimpanzee patrol groups often travel into areas that abut their territorial boundaries (Bygott 1979; Nishida 1979; Goodall 1986) and move about in a wary fashion (Goodall 1986). These raids often involve the killing of a small number of members of the raided group and the capture of females. Occasionally raiding parties from two groups will meet one another. Rather than all-out aggression, both groups often engage in hostile vocalizations and then withdraw (Goodall 1986). However, when two raiding parties meet, violence sometimes erupts, resulting in the extinction of one group. For example, Nishida et al. (1985) provide evidence that raiding behavior in the Mahale Mountains of Tanzania resulted in a larger group extinguishing a smaller group of chimps.

Although the costs and benefits of raiding behavior are not known, it appears to be a good candidate for cooperation via group selection. Between-group selection favors such raids (because they most likely benefit all group members, not just the raiding party participants), yet if raiding is dangerous, selection within groups should favor cheating—i.e., letting others do the raiding, but continuing to reap the benefits.

In-group biasing can be even more powerful (and scary) in humans because it rears its head in even the most trivial decision-making processes. Consider Tajfel's (1970) study of in-group biasing in English teenagers in the late 1960s and early 1970s. In this study, 64 boys who attended the same school were asked to estimate the number of dots flashed on a wall. The subjects were then told that they fell into one of two groups: those that overestimated the number of dots or those that underestimated this number.

Once they learned whether they were dot over- or underestimators, each subject was placed in a room by himself with a series of forms. The forms asked the subjects how they would divide up monetary rewards and penalties between two other boys in the study. The pairs from which a subject could choose were made up of either two individuals from his own group, two from the other group, or one from each group.

The results were striking. When asked to divide up rewards and punishments between two individuals from the same group—either the group the subject belonged to or the one that he did not—rewards and punishments were split fairly. If, however, the choice was between someone from the subject's own group (for example, the dot overestimators) and an individual from the other group (the dot underestimators), the subjects consistently favored members of their own group, despite having no information on the actual identity of who was in either group. Simply knowing that others overestimated dots as they did, even if they never met the overestimators, was sufficient to cause an unequal distribution of monetary rewards and punishments.

It should be noted that a preference for those in one's own group is not restricted to primates. A preference for familiar individuals independent of relatedness has been demonstrated in several species of centrachid fish (Brown and Colgan 1986; Dugatkin and Wilson 1992) and guppies (Magurran et al. 1994; Griffiths and Magurran 1999).

By-product Mutualism

Cooperation via by-product mutualism occurs when animals live in "harsh" environments in which there is an immediate cost or penalty for not acting cooperatively (West-Eberhard 1975; Brown 1983; Mesterton-Gibbons and Dugatkin 1992; Connor 1995). Put simply, in harsh envi-

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ronments, the immediate net benefit of cooperating outweighs that of cheating. When this is not the case, in so-called "mild" environments, cooperation by by-product mutualism is not favored by natural selection.

While relatedness plays a role in the hunting behavior of lions, in many ways cooperative hunting in lions exemplifies by-product mutualism. Lions hunt in groups when they are stalking large predators that could not be taken by a single hunter, but work alone when hunting smaller prey (Scheel and Packer 1991). In the case of lions, large prey items constitute a harsh environment, while smaller prey items fall under the rubric of mild environments.

By-product mutualism adds a new twist to the cognitive prerequisites needed for different forms of cooperation to evolve. In by-product mutualism, neither memory nor recognition of individuals is necessary, and while recognition of categories is needed, it is not the same form of recognition of categories as in other types of cooperation. In this case, individuals need to categorize the environment they are in, rather than something specific about another individual. For example, in the case of lions, individual lions need not categorize other lions, but rather assign the environment to either the "mild" or "harsh" category.

Closing Thoughts

The evolution of cooperation continues to be an area of active research interest in behavioral ecology, yet few attempts have been made to explicitly link work on cooperation to animal cognition. Here we have suggested that one way to begin such work is by examining memory and recognition requirements and abilities with respect to four different types of cooperation. Depending on the specific type of cooperation under study, and the specific demographics and structure of the population under investigation, very different cognitive abilities are required for cooperation to be feasible.

To date, very few studies have examined recognition and memory in the context of cooperation (Dugatkin 1997). This may in part be because much of the modern work on cooperation is intimately linked to game theory models of social behavior (Maynard Smith 1982). These models focus on evolutionarily stable strategies and payoff matrices (Hammerstein 1998) and not on the cognitive prerequisites of cooperation. That is, game theory models predict what sort of behavioral strategy can evolve in a particular social environment without much regard for the cognitive requirements. This is not to say that disclaimers such as "only certain types of animals are likely to be cognitively sophisticated enough to . . ." are lacking in game theory papers on cooperation, but rather that detailed studies of recognition, memory, and cooperation are few and far between (see Dugatkin 1997 for a review).

We hope that this essay will spur the studies needed to truly understand the no-doubt complicated relationship between cooperation and cognition. For many reasons this will be a daunting task, even using the framework we have developed. Many instances of cooperation do not fall neatly into one of the four paths to cooperation, but instead combine aspects of more than one path (Dugatkin 1997). For example, work on blood sharing in vampire bats is often cited as a classic case of cooperation by reciprocity in animals (Wilkinson 1984). Yet it turns out that the vampire bats swapping blood meals are also related (Wilkinson 1987). This makes the vampire case no less interesting, but does raise the question of what sort of cognitive abilities we might expect when reciprocity is tied to relatedness.

Even if we could map out all possible combinations of the four paths to cooperation and make predictions with respect to recognition and memory, there would be hurdles to overcome. Work in comparative psychology as well as evolutionary psychology demonstrates that experiments on memory and recognition in animals are fraught with design problems and often require a

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huge number of controls to shed any light on the details of animal cognition (Balda et al. 1998; Dukas 1998; Shettleworth 1998). Yet rather than view these conceptual and experimental problems as stumbling blocks that make the study of cooperation and cognition impossible, we prefer to think of them as fascinating problems in and of themselves, and part of the tribulations associated with studying anything of real importance in science.

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Empirical and Theoretical Perspectives on Animal Cognition

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