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...there is no fundamental difference between man and the higher mammals in their mental faculties. Charles Darwin (1871, p. 35)

Amanda sits waiting in a nail salon. She is on a day out with her two neighbors Bridget and Camille, who are already being serviced by different attendants. After observing Bridget's body jolt several times, Amanda makes her way over to Camille's attendant for her own service. By using a simple social cue, Amanda has likely saved herself a good bit of pain and may even have established a life-long relationship with the apparently more skilled attendant.

If you replace "nail salon" with "cleaning station", these circumstances apply perfectly well to an instance of social rationality in fish! Cleaner fish (e.g., the cleaner wrasse, *Labroides dimidiatus*) establish cleaning stations to feed on parasites attached to the skin of various species of client fish. Sometimes, though, instead of taking the parasites, the cleaner fish bite a piece of skin or mucus—both of which are preferred to parasites. When this happens, the client fish jolt. These jolts, paired with the client fish chasing the nippy cleaners, provide social cues about the cooperativeness of the cleaners, and client fish use this information when deciding which cleaner to visit (Bshary, 2002). Attending to the behavior, choices, and decision outcomes of others can be beneficial, and this socially savvy behavior is by no means restricted to nail salons and cleaning stations, or even to any particular species or class of animals. Instead, we shall argue that social rationality is a key aspect of the lives of animals.

In the quote introducing this chapter, Darwin (1871) boldly claimed that humans and other animals differ very little in their cognition; a statement that has raised the ire of many scientists (Bolhuis & Wynne, 2009; Penn, Holyoak, & Povinelli, 2008). Rather than stating this continuity as fact, we explore the similarities and differences between humans and animals in the social rationality of their decision making. We find this a fruitful exercise because it can profit researchers of both humans and animals.

Our purpose here is to provide an evolutionary background of social rationality: why do animals attend to the lives of others? To this end, we begin by introducing the importance of social situations for the evolution of behavior. We then take a more process-based approach to social decision making by reviewing, first, the use of simple decision mechanisms such as heuristics or "rules of thumb" by animals, second, the requisite capacities and abilities needed for socially rational behavior, and, third, the influence of the environment (social and otherwise) on these decision mechanisms. Each of these topics could yield a chapter (or book) of its own, so instead of a thorough overview, we provide a brief introduction of animal social rationality and a few key examples of the role of heuristics, cognitive capacities, and the environment.

Evolution and Social Rationality

We begin our journey into the evolution of social rationality with Herbert Simon's (1990) metaphor for boundedly rational decision making: "Human rational behavior (and the rational behavior of all physical symbol systems) is shaped by a scissors whose two blades are the structure of task environments and the computational capabilities of the actor" (p. 7). Though he focused on human behavior, does Simon's scissor metaphor apply equally well to animals? We think so, but the need for this metaphor differs when studying animal behavior. Simon proposed the scissors metaphor because psychologists tend to focus on the mechanisms of the human mind, often neglecting the environment. For students of animal behavior, the bias tends to be reversed: influences of the environment are exceptionally well studied, but actual cognitive mechanisms of behavior receive less attention.

The environment is a critical feature of studying animal behavior because of its importance in natural selection. For a brief recap, there are three requirements for natural selection to operate: variation in characteristics (e.g., beak shape in birds), inheritance of characteristics (e.g., parents pass on genes for beak shape to young), and differential survival and reproduction, or Darwin's (1859) "struggle for existence" (e.g., only

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individuals with certain beak shapes can open available seeds). This struggle for existence occurs in relation to both the physical and social environment. Since "natural selection acts by competition" (Darwin, 1859, p. 472) for food, shelter, mates, and space, the social environment plays a particularly crucial role for the evolution of behavior.

Evolutionary game theory (Maynard Smith, 1982) illustrates the importance of the social environment for animal decision making. This framework provides a tool to explore the strategic component of animal behavior. That is, animals do not choose where to forage, with whom to mate, how to raise offspring, and when to cooperate in a social vacuum. Rather, the consequences of making these decisions depend upon what others in the population do. Evolutionary game theory is similar to standard economic game theory (von Neumann & Morgenstern, 1947), except it focuses on the population level rather than the individual level. Economic game theory assumes that rational agents choose the "best strategy" by computing the appropriate payoffs, given perfect knowledge of the partner's beliefs and behavior. Evolutionary game theory, in contrast, assumes minimal abilities of the agents, embeds them in a population of agents employing different strategies, and lets natural selection choose the best strategy or strategies. In other words, animals implement different possible strategies, but the selection of these strategies takes place through an evolutionary process (Conradt & List, 2009; Stevens, 2008). Evolutionary game theory has enjoyed great success in explaining animal behavior (Dugatkin & Reeve, 1998), perhaps more success than classical economic game theory enjoys for human behavior (Camerer, 2003).

The Social Brain

Despite its success, evolutionary game theory has been limited by its emphasis on behavior and its neglect of the cognitive building blocks required to implement the evolved strategies that may be used in these games. This is a critical void because species vary widely in the cognitive abilities used to solve similar tasks. Take navigation as an example. Ants track scents laid on the ground by other colony members, birds orient with magnetic fields in the earth, and humans follow elaborate maps. These mechanisms, more often than not, efficiently guide the ant, bird, or human to their intended location, yet each requires a very different set of cognitive tools. What can explain these differences in cognition? What selective forces could generate complex and varied cognitive abilities?

Early work on the evolution of animal cognition and intelligence highlighted the role of ecology—an animal's habitat, food, and predators—as a driving force shaping cognition. In particular, food distribution, food extraction, and ranging patterns are correlated with various measurements of brain size in primates (Milton, 1981; Parker & Gibson, 1977). For instance, howler monkeys (*Alouatta palliata*) eat primarily leaves, whereas spider monkeys (*Ateles geoffroyi*) consume more fruit. This difference in diet leads to different cognitive demands for foraging. Leaves are abundant, but fruit, in contrast, is more patchily distributed. Milton (1981) suggested that the spatial and temporal variation associated with foraging for fruit may have selected for more complicated cognition to track the variable environment. In fact, for howler and spider monkeys, as well as primates and other mammals more generally, fruit-eating species have larger brains on average than leaf-eating species. The correlation between foraging ecology and brain size, however, disappears for primates when you factor in body size (Dunbar, 1992), and some argue that a more potent force exists: social relationships.

The *social brain hypothesis* assumes that the complexities of social life require sophisticated mental abilities (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976; see also chapter 1). A special kind of intelligence is required for the ever-changing social demands of maintaining group cohesion, coordinating movement, preserving bonds, forging alliances, tracking cooperation, detecting cheaters, communicating information, manipulating competitors, and in general strategically responding to and interacting with other responding and interacting agents.

Given the demands of social life, the social brain hypothesis predicts that individuals of highly social species will evolve intelligent ways to cope with this complexity. Intelligence is, of course, difficult to define and even trickier to measure and compare across animal species. Though researchers can successfully relate social life to measures of intelligence such as incidence of behavioral innovation, social learning, and tool use (Reader & Laland, 2002), more typically they use the proxies of group size and brain size. For instance, when showing that ecological factors accounted for very little variation in primate brain size, Dunbar (1992) contrasted this finding with a strong correlation between group size and brain size. Specifically, the mean group size correlated with the size of the neocortex relative to the rest of the brain for primates (Figure 1). Dunbar (1998) argued that this relationship did not result from visual, memory, or emotional demands. Rather, relative neocortex size increased with group size because the capacity to gather, update, and manipulate information about social relationships should directly correlate with the number of relationships individuals must track. This is particular relevant for species with fission-fusion social dynamics in which individuals are constantly joining and leaving the group. Such flux may require that individuals constantly track and maintain information on the presence and absence of others and respond appropriately (Aureli et al., 2008).

The social brain hypothesis and fission-fusion dynamics do not only apply to nonhuman primates. Dunbar (1992) used the correlation between group size and relative neocortex size observed for nonhuman primates to predict a social group size for humans. Using a regression equation on data for 38 primate genera, Dunbar predicted a mean group size of 148. Dunbar also found empirical support for this prediction: the average number of people living in 21 surveyed hunger-gatherer societies around the world was 148.4 (Dunbar, 1992). Along similar lines, nonprimate species that show rather enhanced and flexible forms of cognition (e.g., corvids, parrots, elephants, dolphins and whales) are highly social and many exhibit fission-fusion dynamics (Aureli et al., 2008; de Waal & Tyack, 2003). Consequently, several independent cases of group size/brain size correlations provide convergent evidence for the social brain hypothesis.

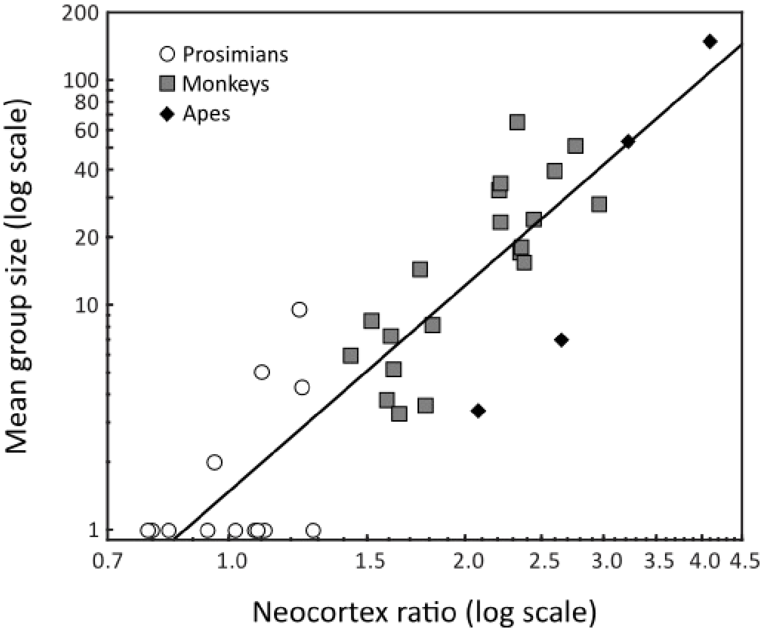

Figure 1. Evidence for the social brain hypothesis. This figure shows the log-log relationship between neocortex ratio (neocortex size relative to the rest of the brain) and mean group size (r^2=0.80 with humans included, upper right diamond). This pattern also holds when apes and monkeys are analyzed separately. Figure redrawn, with human data added, from Dunbar (1992).

Games against Nature

The social brain hypothesis typically implies that strategic games against other individuals drive cognition. Yet, often animals are locked in a constant game against nature to find food, shelter, and a safe place to raise young. Though, at first glance, the struggle against nature appears to lack a social component, even in these situations, animal decisions depend critically on the actions of others. Here, we focus on two ways in which animals interact with others to solve problems in their physical environment. First, they may treat other individuals as sources of information to make individual decisions. Second, they may band together to make collective decisions in the struggle against their physical environment. In both cases, the addition of a social component provides an opportunity to greatly enhance individual decision making.

Using social information. When individuals face uncertainty in their environment, the behavior and actions of other individuals with similar requirements becomes especially useful. Specifically, individuals that can monitor and use the information that other individuals provide—known as “social” or “public” information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005)—are in a position to improve both their decision making speed and accuracy (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003; King & Cowlishaw, 2007). The use of social information can therefore be thought of as a force that promotes the evolution of social living.

Consider a very simple example borrowed from Sumpter (2010). When searching for food, one bird observes another bird with its head down, pecking in the ground. From this observation alone the observer obviously does not know whether this other bird has discovered food or is simply searching for food. However, we know from laboratory studies that when ground-feeding birds (spice finches, *Lonchura punctulata*) have their head down, they have likely found something to eat (Coolen, Giraldeau, & Lavoie, 2001). The proportion of time a bird has its head down indicates the bird’s foraging success. Thus, a bird that follows a simple heuristic “always join a bird with its head down, never join a bird with its head up” will, on average, do better than if it joined at random. Empirical evidence suggests that this is exactly what happens. Using an artificial flock of model birds, some with heads down and others with heads up, Drent and Swierstra (1977) showed that barnacle geese (*Branta leucopsis*) were more likely to land near groups of models where more birds had their heads down: akin to "copying successful individuals" (Allison, 1992; chapter 1).

Despite the adaptive appearance of learning from others, an evolutionary analysis predicts that the advantages of using individual or social learning depends on the level and timing of variability in the environment and the error rates and costs of both types of learning (Boyd & Richerson, 1985). Empirical evidence supports this notion. Individuals switch conditionally between reliance on information which they collect themselves (individual learning) and information provided by others (social learning), according to their respective reliability and cost (van Bergen, Coolen, & Laland, 2004; chapter 17).

A number of other factors can also promote or constrain the use of social information. One such factor is the structure of the social network, that is, the pattern of relationships across members of a group. The spread of information may depend differentially on large-scale network structure such as permanent groups versus ephemeral fission-fusion groupings, or at a finer scale, it can also depend on the social relationships between group members. Social network analysis (Krause, Croft, & James, 2007) can help clarify to what degree this is the case (Figure 2). For instance, individuals with many social contacts might be most influential in information transfer (Lusseau & Newman, 2004).

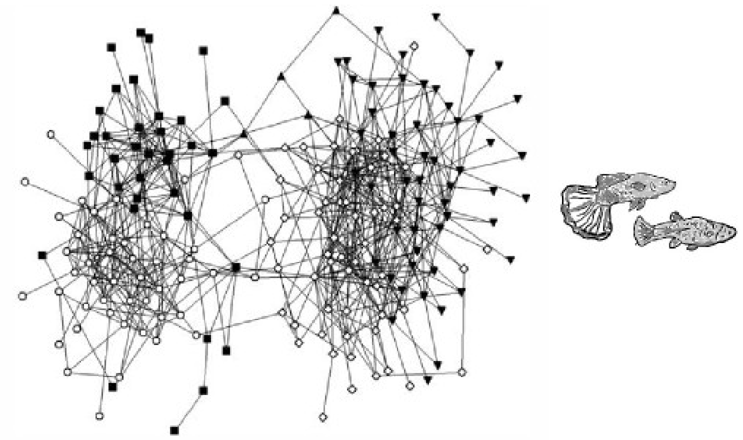

Figure 2. Network structures in fish. Croft et al. (2006) recorded associations between wild guppies (*Poecilia reticulata*) to conduct a social network analysis. Statistics that identify clustering of individuals identified five communities within the pools, represented by filled squares, filled inverted triangles, filled triangles, empty diamonds and empty circles. Figure from Krause et al. (2007).

Group decision making. In addition to parasitizing information from others, animals may pool information and preferences to make decisions in a group. Of interest are situations in which a collective of individuals aims to "outwit nature": how can a collective of individuals increase their chances of finding the correct answer to a problem posed by their environment? Research tackling this question in the social science literature is vast (for examples, see chapters 6 & 7). In contrast, researchers in the natural sciences have only recently considered such questions in detail (for a review, see Conradt & Roper, 2005).

First, groups can improve the accuracy of their decisions by aggregating information across individuals, a principle first highlighted by Sir Francis Galton in 1907. When attending a country fair, Galton observed that one of the attractions was to guess the weight of an ox once slaughtered and dressed. Galton took the answers of the nearly 800 fair goers and computed the average, which turned out to fall within one pound of the right answer (Surowiecki, 2004), even though a random individual taken from within this collective is likely very far from the true answer. This principle has been applied to animal decision making in which error is assumed to be unbiased. For example, for migrating birds that must navigate to a specific location, the average direction of all group members is more likely to be correct than following the direction of any one randomly chosen individual (Figure 3; Simons, 2004), and this has been supported by experiments with pairs of migrating birds (Biro, Sumpter, Meade, & Guilford, 2006). Second, group members can follow the actions of an especially informed leader who can guide groups of naïve individuals to resources they would otherwise not be able to locate (Couzin, Krause, Franks, & Levin, 2005; King, Johnson, & Vugt, 2009). In both scenarios, individuals may be able to tap into this social information by using simple heuristics, or "rules of thumb".

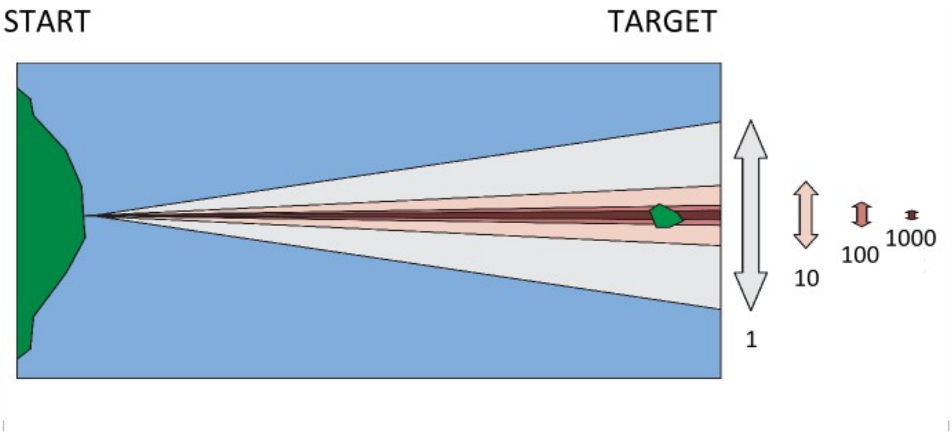

Figure 3. The advantageous effect of large group size on navigational accuracy for a theoretical migrating bird flock. The triangles depict 95% confidence intervals of trajectories for simulations of a single bird and flocks of 10, 100, and 1000 individuals of equal navigational ability. Figure from Simons (2004).

Animal Heuristics or "Rules of Thumb"

The social environment clearly imposes strong selective pressures on animals, but does social complexity necessitate cognitive complexity? Barrett, Henzi, and Rendall (2007) argue no: simple minds can deal with social complexity. Rather than maintaining representations of their complex social (and physical) environments, animals may use "rules of thumb" or simple heuristics to negotiate the complexity (see also chapter 1). This view advocates situating animals in their environments to assess how they might exploit the structure of the environment, closely mirroring the approach taken by the fast and frugal heuristics program (Gigerenzer, Todd, & the ABC Research Group, 1999; Hutchinson & Gigerenzer, 2005), with its focus on ecological rationality (Todd, Gigerenzer, & the ABC Research Group, 2011).

Some of the most fascinating examples of social behavior in animals involve remarkable temporal synchrony: large groups of fireflies fill the trees in Malaysia and all flash their lights in unison, synchronized within 30 ms of each other (Buck & Buck, 1968). Such a high degree of synchrony does not necessitate complex cognition though; simple heuristics suffice. The fireflies simply reset their pacemaker when they see another flash, resulting in a remarkably coordinated outcome. Though the role of heuristics is not universally accepted by researchers of human decision making (see, e.g., the commentaries on Todd & Gigerenzer, 2000), evolutionary biologists describing animal decision making have relied on them for decades.

Hutchinson and Gigerenzer (2005) reviewed some of the heuristics that animals use when foraging, searching for mates, finding and constructing nests, and tracking moving objects. When we say that animals "use a heuristic", we mean that they exhibit a behavior consistent with the use of a heuristic. For instance, when dragonflies pursue and intercept moving prey, they seem to use a simple heuristic: steer to keep the prey in a constant retinal position (Olberg, Worthington, & Venator, 2000). Rather than calculate where the prey will be, the dragonflies simply maintain the prey in a fixed point in their visual field (Figure 4). Interestingly, baseball players use a similar heuristic to catch fly balls—they keep the angle of gaze to the ball constant (McBeath, Shaffer, & Kaiser, 1995). This gaze heuristic (Gigerenzer, 2007) seems to be useful for a variety of organisms to intercept a moving object.

Simple Heuristics

Humans and animals use similar heuristics in non-social domains. Do humans also share heuristics in social domains with other species? Next, we briefly describe a few examples of simple heuristics used by animals in social domains, ranging from mating choices to cooperative behaviors to collective decision making.

Choosing a mate is an important social decision for most animals (chapter 13). Mates provide "good genes" for offspring, as well as potential help in raising young. How should one go about choosing a mate? One strategy might involve assessing information about a potential mate's health, fitness, and care-giving abilities, then carefully weighing each of the attributes to generate a "value" for each mate and choosing the mate with the highest value. A simpler strategy is to copy the mate choices of others. When you see another individual choose a potential mate, then just copy this choice. This occurs in female guppies (*Poecilia reticulata*) in which females are more likely to choose males that they observe near other females (Dugatkin, 1996). In fact, social cues are so strong that they can override previous choices. If females choose male A over male B in an initial choice, they often switched to male B in a second choice, following the observation of another female near male B. Though this may sound rather capricious of these guppies, very similar strategies may be used in humans. When rating the attractiveness of or interest in members of the opposite sex, both men and women rate potential partners as more desirable when they are observed paired with other partners (Place, Todd, Penke, & Asendorpf, 2010; Waynforth, 2007). Consequently, copying the choices of others can be a quick, simple way for humans and animals to select mates.

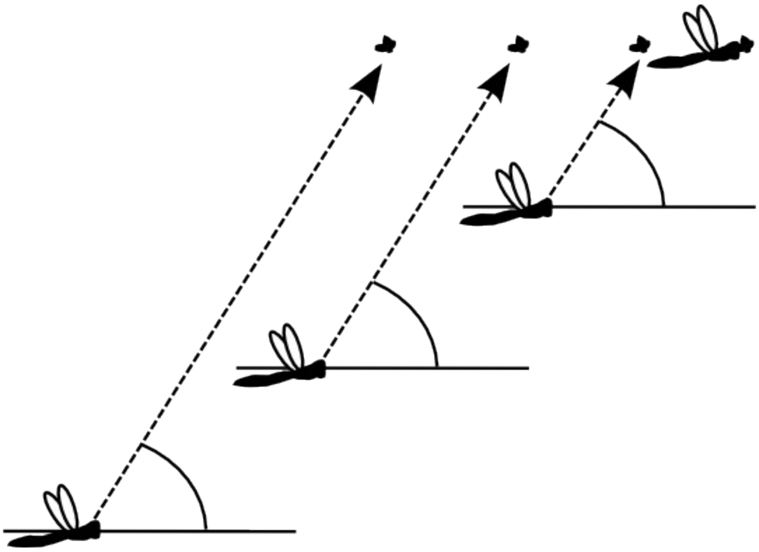

Figure 4. The gaze heuristic in dragonfly foraging. When intercepting flying prey, dragonflies seem to maintain a constant angle of attack. Redrawn from Olberg et al. (2000).

Simple heuristics also apply in cooperative situations (chapter 12). Kin-directed altruism, for instance, implies that individuals can discriminate kin to direct their help appropriately (e.g., help siblings more than cousins). Animals adeptly discriminate kin and use various mechanisms for doing so (Fletcher & Michener, 1987). Common mechanisms used by animals are simple heuristics such as “be nice to individuals near your home” or “help those that you grew up with”. Rather than try to directly assess kinship (a nearly impossible task for many species), these heuristics use cues such as spatial proximity or duration of association, which are often highly correlated with relatedness. They are by no means perfectly correlated, as illustrated by the pervasiveness of brood parasitism (e.g., when cuckoos lay their eggs in other birds’ nests, the hatchlings are often treated as offspring/siblings). Nevertheless, animals use these proxies for kinship to direct help. For instance, Holmes and Sherman (1982) reported an elegant cross-fostering experiment in which newborn ground squirrels (*Spermophilus parryi* and *S. beldingi*) were placed in different nests to be raised by nongenetically related parents. Supporting the familiarity rule, aggression between individuals depended on whether they were raised together rather than on genetic relatedness. A similar pattern of kin discrimination appears in humans in the form of incest taboos. When children in Israeli communes (or *kibbutzim*) are raised in small, age-matched cohorts of both sexes, members of these groups rarely marry each other (Shepher, 1971). This has been suggested as a mechanism to avoid the genetic costs of incest, a potentially strong selective pressure for detecting kin (Lieberman, Tooby, & Cosmides, 2007).

Another simple heuristic used in cooperative situations is tit-for-tat, a heuristic that generates reciprocal altruism (Axelrod & Hamilton, 1981; Trivers, 1971). If interaction partners take turns cooperating, the cooperative action is effectively an investment in the future reciprocated benefits. Tit-for-tat simply starts by cooperating with a partner, then copies the partner’s cooperation or defection in the previous move. Tit-for-tat is a quite simple strategy, and evolutionary simulations suggest that it can outperform pure defection if a pair of individuals interacts often enough (though it is not an evolutionarily stable strategy, Selten & Hammerstein, 1984). Tit-for-tat-like behavior seems to be fairly widespread in human cooperative interactions (Ostrom & Walker, 2003); however, its existence is less well supported in animals. Despite its seeming simplicity, the cognitive building blocks required to implement it are not trivial (see Cognitive Building Blocks for Simple Heuristics in a Social World). Thus, here we have a case in which humans seem to use this simple heuristic, but animals may not.

The heuristics we describe so far operate among relatively few individuals, but heuristics can also play an important role in collective animal behavior that can involve hundreds or thousands of individuals. For instance, how do collections of individuals decide when to move towards a specific resource (e.g., foraging site or waterhole) or switch behaviors (e.g., from resting to foraging) as a group? One way of achieving this is for individuals to respond only when they see a threshold number of individuals (a quorum) or a majority of conspecifics performing a particular behavior or heading in a specific direction, even if they themselves are not motivated to do so. This way, individuals have a mechanism for maintaining group cohesion and achieving group decisions. Indeed, such responses are common in animal groups across a variety of taxa from ants to fish to primates (Sumpter, 2010), and copying successful individuals, copying successful behaviors, and copying the majority are all heuristics that usefully apply to human social settings (Mesoudi, 2008). Collective problems, and group movement in particular, offer a number of instances in which animal use simple heuristics in social domains.

Take a situation we humans encounter regularly as social animals. When walking down a busy street in rush hour, you balance your desire to reach your destination with your local environment—the motion and positions of other nearby pedestrians. You may not be able to see much more than a couple of people ahead of you, and the movements of you and your neighbors may appear disorganized. However, if you look down upon the crowd, you would see some very obvious patterns of behavior. For instance, the crowd may have assorted themselves into a series of lanes, each composed of people moving in the same direction (Couzin & Krause, 2003; Helbing & Molnar, 1995). This allows the pedestrians to move toward their destination quickly and often more accurately. The mechanism for such lane formation is surprisingly simple. Given a sufficiently high traffic flow, individuals balance their desire to move in an intended direction with a desire not to collide with other people. Individuals will, by chance, fall in behind another individual moving in the same direction, resulting in a "stable" state. Individuals may also actively seek out others moving in the same direction, facilitating this process (Couzin & Krause, 2003).

Such "self-organization", where a global pattern emerges as a consequence of interactions among individuals responding to local information, is surprisingly common in human and animal aggregations alike (Camazine et al., 2001; Sumpter, 2006). The evolutionary function of and proximate mechanisms influencing these swirling, pulsing masses of individuals are only now beginning to be fully understood. It is possible that the huge variety of shapes and motions of animal groups that we see in animal aggregations results from only small variations in heuristics followed by individual group members. For instance, Couzin et al. (2002) proposed a model in which individual animals follow three simple heuristics "move away from very nearby neighbors", "adopt the same direction as those that are close by", and "avoid becoming isolated" (Figure 5A). Their model showed that three very different collective patterns of behavior could emerge as a consequence of only small adjustments to just one of these three rules: the radius over which individuals adopt the same direction with one another (Figure 5B-D).

Do models like those of Couzin et al. (2002) correspond to what we see in nature? Are these simple rules responsible for reproducing these complex collective behaviors? In fact, very few model validations exist. One recent attempt to test the validity of such models was undertaken by Ballereni et al. (2008). They measured three-dimensional positions of individual starlings in flocks containing thousands of individuals, and their analyses suggest that many of these zone-based models accurately reflect empirical observations. For instance, they showed that individual birds had a well-defined repulsion zone (Figure 5A), which was equal in diameter to the average wing span of the birds. This exclusion zone was extremely stable across flocks. However, they also found that though birds accounted for their physical distance to their neighbors, for more distant birds, the actual distances did not matter. Instead, individual birds interacted with (i.e., responded to behaviors from) up to its seventh neighbor, wherever its location in space. Studies like Ballereni et al. are rare, and though theoretical models continue to be developed, empirical tests lag behind. Careful empirical work is needed because similar patterns of behavior can result from very different underlying heuristics. For example, the coordinated mass migration in juvenile desert locusts (*Schistocerca gregaria*) can look very similar to patterns of flocking in birds or schooling fish, but these insects do not rely on zone-based heuristics. Instead, the coordinated mass migration is influenced strongly by cannibalistic interactions: abdominal biting and the sight of others approach from behind triggers movement, creating an autocatalytic feedback that results in directed mass migration (Bazazi et al., 2008). It is therefore important that these theoretical models continue to be tested across different animal taxa —including humans (Dyer, Johansson, Helbing, Couzin, & Krause, 2009) to validate their basic assumptions concerning the likely heuristics being employed.

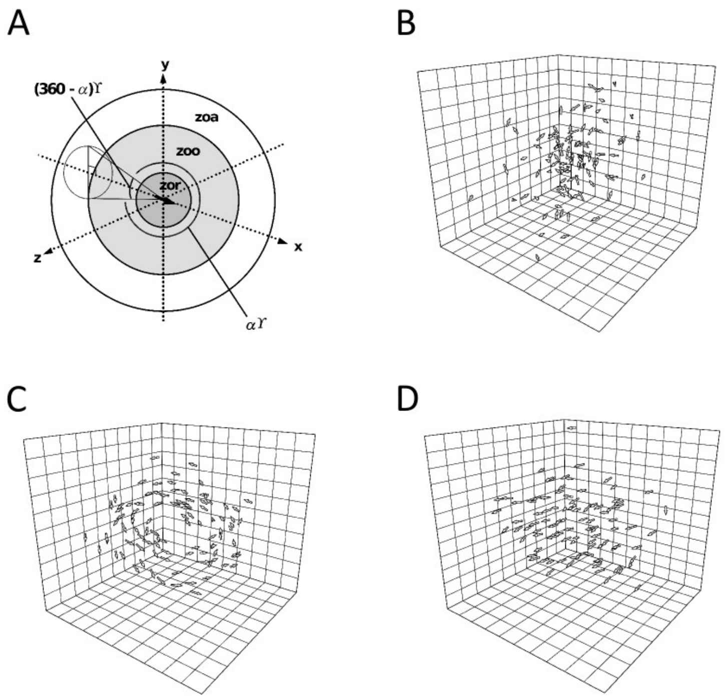

Figure 5. Couzin et al.'s (2002) model of collective behavior. A) An illustration of the rules governing an individual in the model shows the individual centered at the origin: **zor** is the zone of repulsion; **zoo** is the zone of orientation; **zoa**, is the zone of attraction. B) Couzin's models showed that if individual agents had attraction to group-mates, but low, or no, zone of orientation (**zoo**), they formed a "swarm". In this swarm state even though individuals tended to rotate around the group center, they did so in different orientations. C) As the size of the **zoo** was increased, however, the group formed a "torus" in which the individuals perpetually rotated around an empty core and the direction of rotation was random. D) If **zoo** was increased further, the group initially adopted a "dynamic parallel" conformation in which the agents' movements were highly aligned in a single direction. Figure from Couzin et al. (2002).

Cognitive Building Blocks for Simple Heuristics in the Social World

So far, we have referred to some of the simple heuristics in a rather vague manner. For heuristics to be useful in the study of cognition, however, they must be specified precisely such that they can actually model the process of decision making (Gigerenzer, 1996). To fully specify a model of a cognitive process, one must carefully consider the building blocks of evolved capacities required to implement the process. Different capacities are needed for different heuristics, and even other heuristics may act as building blocks (Todd & Gigerenzer, 2007). The gaze heuristic that we described earlier, for instance, requires the capacity to track moving objects. Though this may seem easy to us and trivial from a process perspective, it is no small feat for a computer program to track moving objects. Thus, considering the cognitive building blocks required for heuristics can illuminate our understanding of the processes involved in decision making. It can also allow us to make predictions about the evolutionary feasibility of heuristics.

If specific building blocks are required for a particular heuristic, then we can screen either individuals or species for this requisite building block and make predictions about the ability to implement a particular heuristic. Cross-sectional or longitudinal studies across the lifespan could provide key data to explore these ideas. For instance, children younger than four years old seem to have a less than fully developed capacity to make inferences about the beliefs of others (Wellman & Brandone, 2009). This would suggest that strategies requiring inferring the beliefs of others would not be feasible for young children or populations with a deficit in this capacity (such as autistic individuals). Mindreading is a requisite building block for economic game theory because full rationality necessitates that I know that you know that I know that you know, *ad infinitum* (McCabe, Smith, & LePore, 2000). In fact, children improve in their strategic reasoning in games as they get older (Perner, 1979; chapter 10), mirroring the development of their understanding of mental states in others. Comparing species can also allow us to explore how building blocks are assembled to generate heuristics. For instance, animals vary in their ability to wait for delayed rewards (Stevens & Stephens, 2009), so we would predict that only species demonstrating patience could implement strategic decision depending on future payoffs, like reciprocity.

It is important to trace heuristics back to their building blocks because it can give us leverage on what kinds of strategies might actually evolve (Stevens, 2008). Currently, evolutionary models that test the evolutionary stability of heuristics neglect the cognitive building blocks required to implement these strategies. Without an understanding of the cognition needed to use these strategies, these models lack a realistic background with which to test the evolution of behavior. We illustrate this contention with an analysis of the building blocks required for the well studied heuristic tit-for-tat.

The Building Blocks of Tit-for-Tat

Tit-for-tat is a simple heuristic that achieves cooperation by copying a partner's action in the last interaction. Despite its apparent simplicity, when we explore the cognitive building blocks required to implement tit-for-tat, we see that it is not as simple as it looks. If other animals lack the requisite building blocks, this may explain why tit-for-tat-like strategies are rare outside of humans (Hammerstein, 2003; Stevens & Hauser, 2004).

Trivers' (1971) original formulation of reciprocal altruism proposed three requirements for its evolution: First, the reciprocated benefit must outweigh the immediate cost, second, individuals must interact repeatedly, and third, individuals must recognize each other. These requirements, however, most likely underestimate the cognitive tools necessary for both developing and maintaining a system of stable reciprocity. In particular, if a time delay exists between the cost of a cooperative act and the benefit of reciprocated cooperation, this introduces a number of cognitive challenges. These challenges may apply to many implementations of reciprocal altruism—here we focus on the cognitive building blocks used by tit-for-tat.

Individual recognition. Like kin-directed altruism, tit-for-tat requires targeting specific other individuals for cooperation. Therefore, the delayed, contingent response required for tit-for-tat necessitates that individuals can distinguish different partners. Mechanisms for individual recognition appear to be quite common in animals from wasps to sheep and can use visual, acoustic, and olfactory cues (Tibbetts & Dale, 2007). Consequently, in explaining the paucity of evidence for tit-for-tat in animals, one cannot appeal to individual recognition as a constraint.

Number, amount, and time. Numerical abilities can play a key role in tit-for-tat when individuals must precisely quantify the reward amounts being reciprocated. If a cooperative act is fixed and discrete (e.g., giving an alarm call), quantification skills are unnecessary. But if variation exists in the amount of benefit in question, then quantification becomes quite important. Accurate quantification in animals is limited to small magnitudes; at larger magnitudes, quantification abilities resort to a more approximate system (Figure 6A; Cantlon, Platt, & Brannon, 2009; Feigenson, Dehaene, & Spelke, 2004). Thus, when engaging in tit-for-tat, most animals will either be limited to small numbers of objects in cases where the exchange must be precise (a banana for a banana), or they will be freed from this constraint where approximate exchanges are tolerated. The same prediction holds for cases in which the currency is time, such as the duration of a grooming bout. If one monkey grooms another for 10 minutes, the groomer will most likely accept as fair exchange a reciprocated grooming bout of between 8-12 minutes. As reward quantity and time magnitudes increase, quantification accuracy decreases, making equitable exchange of cooperation more difficult and leaving opportunities for cheaters to exploit the judgment errors.

Patience. Reciprocal altruism is a problem of patience: can an individual inhibit the choice of an immediate, small reward of defection to gain the long-term, larger benefits from cooperation? Indeed, a number of researchers have predicted that lack of patience prevents the establishment of cooperation (Green, Price, & Hamburger, 1995; Rachlin, 2000). Experimental data on variation in human patience and cooperation validate the view that a preference for immediate rewards may inhibit reciprocity. Patience correlates with cooperation in humans such that individuals who can wait for delayed gains also cooperate more frequently (Harris & Madden, 2002). In parallel, captive blue jays (*Cyanocitta cristata*)—a small, North American corvid—showed stable cooperation against reciprocators in an altruistic cooperation game only following an experimental manipulation that increased their patience (Stephens, McLinn, & Stevens, 2002). This connection between patience and cooperation is particularly problematic given the relatively impulsive preferences shown by animals (Figure 6B; Stevens & Stephens, 2009). Implementing tit-for-tat requires overcoming a very strong drive for immediate payoffs.

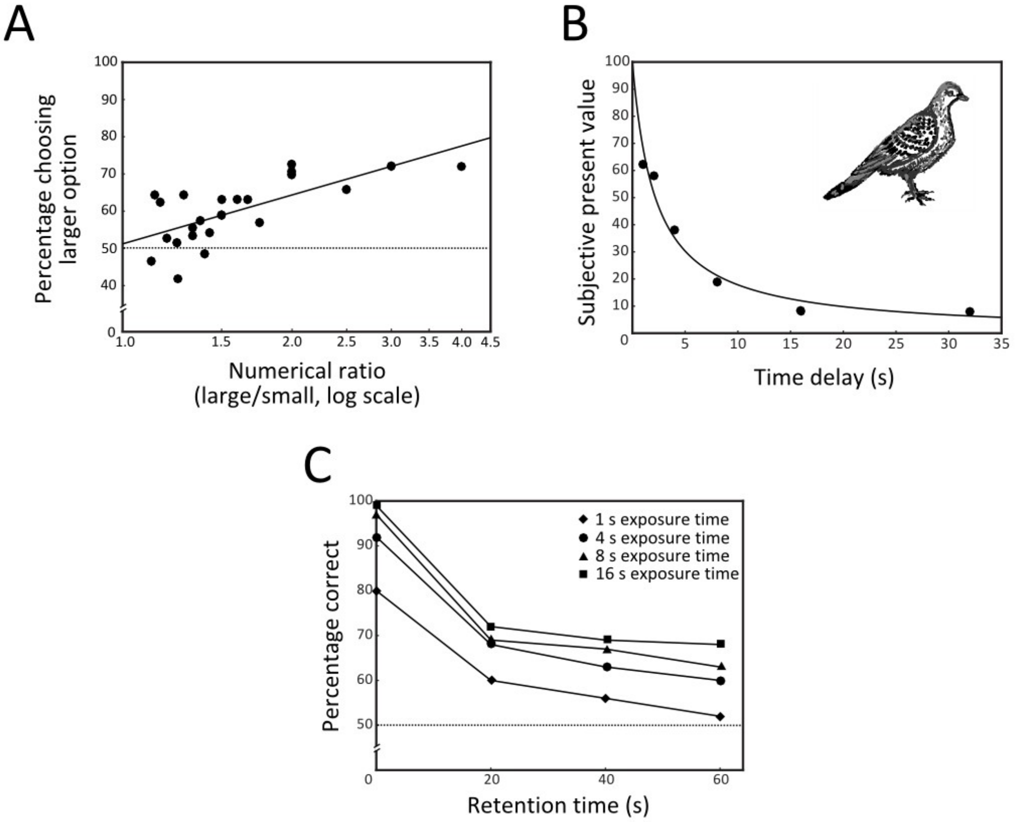

Figure 6. Number, patience, and memory in pigeons (*Columba livia*). Experimental psychologists have tested pigeons in a number of tasks that tap possible cognitive building blocks required for tit-for-tat. A) In a task in which pigeons are reinforced for choosing the larger of two sets of dots, the ratio between the number of dots (large/small) influences performance. As the number of dots increases, the numerical ratio decreases, and the pigeons drop to chance performance. Figure redrawn from Emmerton (2001). B) In temporal discounting tasks, pigeons must choose between waiting a short time for a small amount of food and waiting a longer time for a larger amount of food. When plotting the present value of a delayed reward, the pigeons show a steep drop in value over very short time delays. A reward loses about half of its value when delayed 3-5 s. Figure redrawn from Green et al. (2004). C) Pigeon memory is tested with a delayed matching to sample task in which the subject is shown a stimulus and after some delay must match that stimulus. Longer retention times (time between removing the stimulus and presenting choices) degrades their ability to correctly match the stimulus. Increasing the exposure time to the stimulus aids performance, as illustrated by separate lines on the graph. Figure redrawn from Grant (1976).

Memory. Because tit-for-tat requires tracking a partner's last interaction, two types of memory can implement this requirement. The simplest requires a single memory "slot" for a partner that can be replaced with "cooperated" or "defected". This is effectively the memory system assumed in models of cooperation (e.g., Axelrod & Hamilton, 1981). The other memory system that could implement tit-for-tat is episodic memory—the ability to recall specific episodes from the past (Tulving, 2002). In this case, episodic memory recalls an event ("what") performed by an agent ("who") at a particular time ("when"). Thus, for tit-for-tat, episodic memory can be used to recall whether a partner cooperated or defected in the last interaction. Though animals seem to exhibit episodic-like memory (Clayton, Russell, & Dickinson, 2009), it is not clear how long these memories are retained. Because memory degrades fairly rapidly over time, previous interactions can interfere with recalling the most recent at long intervals between interactions (Figure 6C). Moreover, real agents do not just interact with a single partner, but they are embedded in a large social network of partners. Tracking reciprocal obligations with the extensive social network found in many species may place a computationally intensive burden on memory systems. Although few studies examine learning and memory constraints in cooperation (but see Milinski & Wedekind, 1998; Winkler, Jonas, & Rudolph, 2008), studies of human memory suggest that these constraints may pose challenges for tit-for-tat. In particular, people have a difficult time accurately tracking past cooperation, and this error increases with more partners to track (Stevens, Volstorf, Schooler, & Rieskamp, unpublished data). Despite the apparent simplicity of the memory system required for tit-for-tat, in actuality, robust memory can highly constrain its implementation.

By exploring the cognitive building blocks, we discover, surprisingly, that the simple-looking heuristic tit-for-tat may not be as simple to implement as it appears. This cautionary tale highlights the importance of carefully considering the cognitive machinery required for various decision strategies, especially in evolutionary models.

The Role of the Environment

Thus far, we have considered how social pressures influence decisions. This is very much in line with the idea of ecological rationality, where decision rules are adapted to the structure of the physical and social environment. Ecological rationality in humans, however, often does not refer to adaptation over an evolutionary time frame but rather to responding to changes in their current physical and social environment in real time. Real-time, adaptive decision making is not unique to humans though; a number of animal examples exist.

To understand the conditions necessary for real-time adaptive decisions to evolve, we must consider the relative costs and benefits for alternative strategies. This "payoff structure" is especially critical from an evolutionary game theoretic perspective. Animals are, in fact, quite sensitive to payoff structures. In laboratory experiments, blue jays played experimental games with other individuals, and, depending on their choices and the choices of their partners, they received different amounts of food (Stevens & Stephens, 2004). Varying the payoffs in these cooperative games tested how the jays responded to the reward contingencies in the environment. Their responses were clearly context dependent and adaptive: the jays cooperated in mutualism situations, defected in an altruistic cooperation game, and cooperated in a game in which each player had to rely on its partner to receive any food (Stevens & Stephens, 2004).

The jays clearly learned the environmental contingencies of the social games and respond appropriately. Does this response, however, carry over into more naturalistic situations? Work on primates has explored the importance of the physical distribution of food in their environment on cooperation. Specifically, researchers have tested to what extent primates respond to the divisibility of food resources. Divisibility of food is important because highly divisible food can be difficult to monopolize by a single individual, hence food sharing may be more likely. Chimpanzees show clear sensitivity to food divisibility in a number of ways, including by increasing recruitment calls, levels of harassment, and cooperative problem solving when food is divisible compared to monopolizable (Hauser, Teixidor, Fields, & Flaherty, 1993; Melis, Hare, & Tomasello, 2006; Stevens, 2004). Thus, animals carefully monitor their physical environment when making social decisions.

As we have seen, the social environment may provide crucial pressures in shaping individual decision strategies, and this fact becomes particularly relevant when considering decision making under uncertainty; that is, in situations in which animals must choose between options that vary in their probability of receipt. Sensitivity to uncertainty has a long history in the study of animal behavior (Kacelnik & Bateson, 1996), and food caching provides a useful example of how social competition generates uncertainty.

The harsh conditions of winter can wreak havoc on the foraging strategies of many creatures. The freezing temperatures, blustery winds, and blanketing snowfalls make foraging very difficult, especially when food is scarce. Many animals have solved this problem by caching—an individual collects and hides food, and then returns to it at a later time (Smith & Reichman, 1984). Caching offers an extraordinary case of patience in animals, because the cachers may not return for months to retrieve the food. They forgo immediate consumption to save food for a time in which it will be even more valuable. This is a risky strategy, however, since caches can be pilfered if others observe an individual either storing or retrieving a food item. Therefore, social competitors can provide an even stronger source of uncertainty than the physical environment.

Scrub jays (*Aphelocoma californica*), social birds of the corvid family, engage in complicated food caching in an uncertain environment, employing different caching strategies depending on the social situation (Clayton, Dally, & Emery, 2007; Clayton & Emery, 2009). A novel experimental set-up developed by Emery and Clayton (2001) tested to what extent scrub jays protected their cache. Laboratory jays were allowed to cache either in private (when another bird's view was obscured) or while a another bird was watching, and then they could recover their caches in private. Emery and Clayton's results demonstrated that the jays remembered the social context of specific past events, and adjusted future behavior accordingly by re-caching food that another individual observed (Figure 7). Other experiments showed that the scrub jays also remembered which individual watched them during particular caching events and as a consequence altered their re-caching behavior accordingly by increasing re-caching when dominants were observing (Dally, Emery, & Clayton, 2006). Such experiments demonstrate that animals carefully attend and respond to their social environment by attributing knowledge to conspecifics, utilizing this information in their own decision making, and planning for the future, all the while considering the actions and behaviors of others. How do these findings fit into our comparison between humans and animals in the social rationality of their decision making?

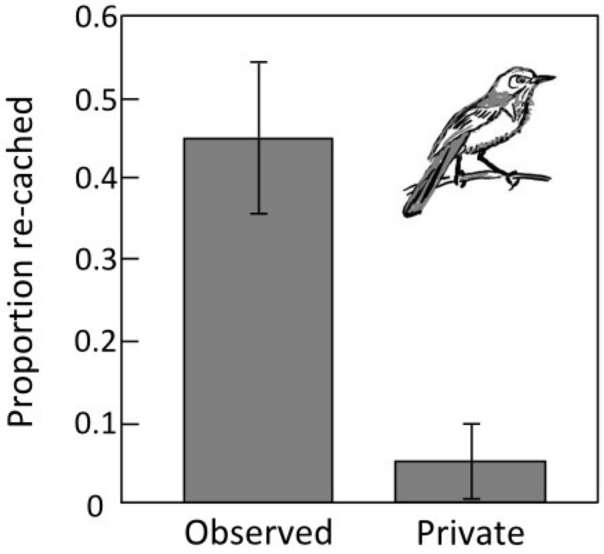

Figure 7. Attention to the social environment in scrub jays. When observed caching by other individuals, scrub jays are much more likely to re-cache the food compared to when they cache in private. Error bars represent standard error of the mean. Figure redrawn from Emery & Clayton (2001).

Such socio-cognitive abilities are often thought to be uniquely human, since, as we have seen argued throughout his book, humans must deal with high cognitive demands in their social worlds. Nevertheless, this socio-cognitive model applies to corvids, and evidence from other taxa which differ vastly in terms of their shared evolutionary history (nonhuman primates: Byrne & Corp, 2004; cetaceans: Marino, 2002) suggest that these abilities must have arisen independently multiple times. For instance, a common ancestor to mammals and birds lived over 280 million years ago, and the two taxa have very different brains (Emery & Clayton, 2004). Thus, although species may differ vastly in their morphology and physiology, where environmental pressures demanded sociality and competition for resources demanded alliances, cooperation, and deception, selection favored "socially intelligent" animals, humans and otherwise.

Conclusion

The social milieu plays a critical role in the evolution of decision making. It requires strategically responding to others and affords the opportunity to use social information and make collective decisions. These features make the social environment a strong selective force shaping decision making and cognition. In this chapter, we have emphasized three key components of social rationality in animals. First, we agree with Barrett et al. (2007) that a complicated social environment does not necessarily require complicated cognition. Instead, simple heuristics can be quite useful for organisms and can result in rather sophisticated social behaviors. From mating to cooperation to self-organized group decision making, heuristics are a common means to navigate the social terrain. Many heuristics are used by both humans and other animals (e.g., mate copying, gaze heuristic), whereas others may not be used very frequently by other animals (e.g., tit-for-tat). Second, in part to explain this variation in the use of different heuristics, we must clearly delineate the cognitive building blocks required for heuristics. This will help narrow down the space of possible heuristics to an implementable set and provides predictions about what species or individuals should be able to use particular heuristics. We saw, for instance, that some relatively simple-sounding heuristics such as tit-for-tat actually require more sophisticated building blocks than may be assumed at first glance, including precise quantification, patience, and accurate memory. The lack of one or more of these building blocks in animal species may explain the relative dearth of evidence for tit-for-tat in nonhumans. Finally, the role of the physical and social environment is critical for social rationality in animals. We focused on how social interactions influence behavior usually considered individual decision making, such as decision making under uncertainty. The social world of an organism, composed of conspecifics and other species, is a constant source of uncertainty. Therefore, including the social environment is crucial when exploring the ecological rationality of simple heuristics.

The examples given here, as well as those in Hutchinson and Gigerenzer (2005), demonstrate that the application of bounded, ecological, and social rationality apply across the animal kingdom, including, of course, humans. This should give some leverage to the study of human decision making because the animal literature can provide fresh ideas for heuristics and other decision processes that may be relevant to human decision making (e.g., Hutchinson, Wilke, & Todd, 2008; Wilke, Hutchinson, Todd, & Czienskowski, 2009). The animal literature is particularly useful for testing questions of ecological rationality because species have evolved in different environments, which may shape their decision processes differently. Thus, one can compare decisions across species with predictions based on their ecology (Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008; Rosati, Stevens, Hare, & Hauser, 2007; Stevens, Hallinan, & Hauser, 2005).

The connection between evolution and cognition is a two-way street, however. Not only can psychologists profit from an evolutionary perspective, but biologists should include cognition in their models of behavior. Evolutionary models that plug in appropriate cognitive building blocks for different species can investigate what types of strategies could have evolved given the constraints of the cognitive system. This combination of the evolutionary and cognitive aspects of decision making, we believe, addresses the spirit of Simon's scissors by welding together the study of the environment and the mind.

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