CHAPTER

26

The Ecology and Evolution of Social Behavior and Cognition in Primates

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Abstract

The social lives of animals present them with a constant yet varying series of challenges that they must solve daily if they want to survive and reproduce. An evolutionary approach to the evolution of social behavior and cognition predicts the convergent emergence of similar patterns and abilities in animal species facing similar challenges, as well as the emergence of a large diversity of behavioral and cognitive abilities within species facing different socio-ecological challenges. In primates, evidence supporting these predictions contradicts a Cartesian approach that many psychologists have adopted favoring captive studies and minimizing the role of experience and ecology. Social grouping is largely the result of a balance between increased predation protection, which is higher in larger groups, and decreased intragroup feeding competition, which is less intense in smaller groups. However, within such optimally sized groups, a great deal of flexibility in how social life can be organized is still possible. Cooperation, altruism, and reciprocity are observed with different levels of prevalence by individuals living in different ecological niches. In many monkeys and chimpanzees, we see that ecological factors play a decisive role in favoring the evolution of cooperation and altruism. The underlying cognitive abilities required to master them will develop according to how important the abilities are for the survival of the individuals. Different aspects of the ecological niche select for different abilities, which prevents a simple model of the evolution of social behavior and cognition. As a rule, the captive environment, a habitat that is particularly unchallenging and safe, selects for less demanding social cognitive development in many primate species, including humans. If we want to gain a better understanding of the evolution of social behavior and cognition, more research should be directed toward primates that face different types and levels of ecological challenges.

Key Words: ecology, sociality, cooperation, altruism, ecological validity, primates, chimpanzees

Introduction

Darwinian ideas of continuity between all forms of life due to common ancestry are to this day hard for some to swallow. If evolutionary thinking has reached a consensus about anatomy, genetics, development, and neuroscience, it has remained very controversial when it comes to cognitive and mental abilities (e.g., Barrett, Henzi, & Rendall, 2007; Boesch 2007, 2010; Cheney & Seyfarth, 2007; de Waal, 2001; Hauser 2006, Penn, Holyoak, & Povinelli, 2008; Povinelli, 2000; Shettleworth, 1998; Tomasello, Carpenter, Call, Behne, & Moll 2005). Two main approaches to comparative behavioral and cognitive studies have dominated. The first follows a Darwinian approach, which endorses an open and unbiased search for similarities between species living in their natural environments. Animals have interacted with the world for generations and have needed to successfully exploit the structure of their environment to survive. Therefore, natural selection has favored behavioral and cognitive mechanisms that have enabled individuals to cope with life in their particular ecological niches. As a result, it is not unexpected that they may have different skills than humans and be able to perform in specific domains better than us, but this need not manifest itself in other domains (Barrett, Henzi, & Rendall 2007; Boesch, 2007, 2008, 2010; Cheney & Seyfarth 1990, 2007; Emery & Clayton 2004; de Waal 2001, 2008; de Waal & Ferrari 2010, Fitch, Huber, & Bugnyar, 2010; Shettleworth, 1998). The second approach follows a Cartesian view, which assigns much less importance to ecology and experience in the development of social behaviors and cognitive skills, and it concentrates instead on the presence of human cognitive abilities in other animal species living in human-made environments (e.g., Moll & Tomasello, 2007; Penn et al., 2008; Povinelli, 2000; Suddendorf & Corballis, 2007; Tomasello et al., 2005; Wolpert 2007). This has resulted in a confusing and contradictory series of claims and counterclaims in the literature on cognitive faculties in primates, which has made this literature very difficult for external readers to understand.

The distinction between a Darwinian and a Cartesian approach is also visible in the attitudes toward the continuity or discontinuity of behavioral and cognitive traits in the animal kingdom. The evolutionary approach predicts continuity in the animal kingdom, including between humans and our closest living relative, the chimpanzee. In particular, possibly unique human traits are expected to have a long evolutionary history, and, therefore, comparative studies are essential in order to understand how such traits evolved and what factors promoted them. In addition, cognitive traits are viewed as adaptations to particular socio-ecological selection pressures on top of what is possible given the evolutionary constraints, including the morphological, physiological, and genetic characteristics of the species considered. The Cartesian approach tends to postulate a qualitative difference within the animal kingdom by which humans distinguish themselves from all other living species in several important traits. Following Descartes' propositions, animals are rigidly programmed and the influence of socio-ecological conditions on the development of behavioral and cognitive traits is minimal to negligible (see Figure 26.1). This explains why evolutionary researchers view captive studies with great caution and critical minds (Barrett et al., 2007; Boesch, 2007, 2010; Cheney & Seyfarth, 2007; de Waal, 2001), whereas, for those who support the Cartesian approach, results of captive studies are accepted uncritically as they are considered most reliable due to their greater detail and better control of possible confounding factors (Hauser, 2000, 2006; Penn et al., 2008; Tomasello & Call, 1997; Tomasello et al., 2005). In reality, experience has proven to be essential for the development of behavioral and cognitive abilities in many different species, such as food-storing bird species, like the Clark's nutcracker (Shettleworth, 1998), macaque and rhesus monkeys (Harlow & Harlow, 1962; Kempes, Den Heijer, Korteweg, Louwerse, & Sterck, 2009; Mason 1978; Mathew et al., 2003; Sanchez, Hearn, Do, Rilling, & Herndon, 1998; Sanchez, Ladd, & Plotsky, 2001), chimpanzees (Gardner & Gardner, 1989), and humans (Berry, Poortinga, Segall, & Dasen, 2002; Gordon, 2004; Fox, Levitt, & Nelson, 2010; Nelson et al., 2007; Smyke, Zeanah, Fox, Nelson, & Guthrie, 2010). In full support of a Darwinian approach that stresses the importance of socio-ecological conditions, many studies have documented the long-term effect of early experience on brain development, brain activity, and cognitive abilities. For example, bonnet macaques exposed to varying degrees of difficulty in accessing food at an early age have been shown to present long-lasting alterations in the functioning of the prefrontal cortex and cognitive functions (reviewed in Sanchez et al., 2001; Mathew et al., 2003). Similarly, children who were institutionalized for extended periods early in life have shown deficits in specific aspects of visual attention and memory as well as visually mediated learning (Pollack et al., 2010). Models of the role of experience in neural development and mounting information on molecular processes in neural plasticity indicate that neural activities (i.e., activity-dependent processes) are critical to brain development (Fox et al., 2010). This implies that in addition to the stimuli available in the environment, active engagement of the environment may be essential in order for some aspects of cognitive development to occur (Greenfield, 1999; Smyke et al., 2010). Furthermore, an important effect of experience later in life on general intelligence has also recently been shown in birds, mice, and humans (Emery & Clayton, 2004; Jaeggi, Buschkuehl, Jonides & Perrig 2008; Light et al., 2010).

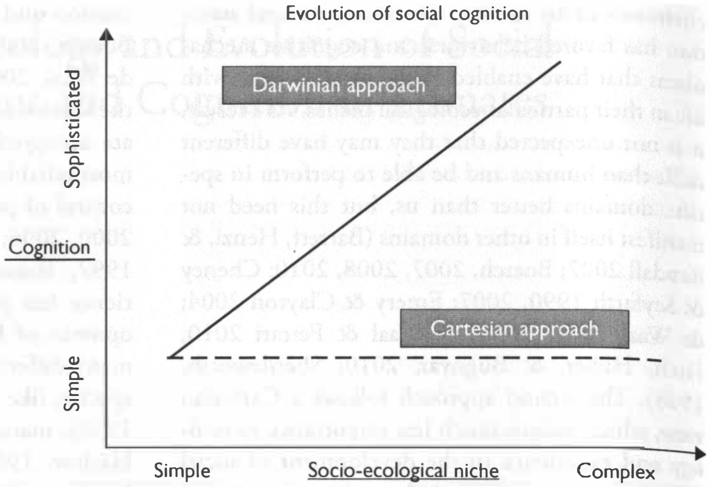

Figure 26.1 Schematic illustration of the predictions of two theoretical approaches to the evolution of social cognition. The Darwinian approach predicts that animals adapt to the socio-ecological conditions they face and will develop more sophisticated abilities while living under more challenging conditions, while a Cartesian approach expects very limited effects of ecological conditions on individual cognition and therefore considers captive studies to be generally valid.

It is important to be aware of these different approaches because some social behavioral and cognitive traits have recently been proposed to be distinctive traits that characterize humans and separate us from all other living animals. These traits include extended cooperation, altruism, altruistic punishment, empathy, and concerns about welfare for others (Fehr and Gächter 2002; Hauser 2006; Hrdy 2009; Penn et al., 2008; Tomasello et al., 2005; Silk et al., 2005). Because most data supporting such claims come from captive studies in which all individuals have been living in deprived ecological conditions and artificial social groups, the uncritical acceptance of such claims by some is surprising. A detailed review of such claims has been made in this volume by Silk and House for altruism (chapter 20), and by Warneken and Melis for cooperation (chapter 21). Therefore, in this chapter, I will restrict myself to reviewing the evidence for social behavioral evolution in wild populations of primates and stress how an evolutionary approach to the question, "What makes us human?" can promote unbiased and ecologically valid answers.

An evolutionary approach views behavior and cognition as adaptive responses to the ecological challenges faced by the individuals (Barrett et al., 2007; Boesch 2005, 2007, 2010; Cheney and Seyfarth 1990, 2007; de Waal 2001; Fitch et al., 2010; Shettleworth 1998). Following such an approach, more demanding socio-ecological challenges faced by individuals of different animal species will select for more sophisticated social behavior and cognitive abilities and lead to important convergent evolution. Second, animal species including humans that face more new socio-ecological challenges will acquire different behavioral and cognitive solutions. Among the primates, humans and chimpanzees have adapted to the largest number of different environmental conditions and are, therefore, predicted to adopt more diverse behavioral and cognitive solutions (Boesch, 2009).

Evolution of Social Grouping

Individuals are expected to adapt to the living conditions they are facing in order to maximize their survival and reproductive outputs. Group living has been considered to be such an adaptation, one that permits the reaction to situations in which lone individuals fare worse than individuals in groups. Generally, two types of factors are proposed to favor social grouping. First, predation pressure is considered to be the main factor that brings animals together, as lone individuals will always suffer higher risks than two or more individuals together (this is called the dilution effect, because two individuals are 50 percent less likely to be caught than when alone, three individuals are 66 percent less likely, and so on) (e.g., Alcock, 1989; Krebs & Davies, 1991). In addition, individuals in groups will gain advantages as a result of information provided by other group members, for example, about predator presence or food-patch distribution. On the other hand, feeding competition will always be higher in groups than for lone individuals, and this will lead to the emergence of optimal group size rather than maximum group size (e.g., Krebs & Davies, 1991). This interplay of ecological factors favoring and limiting group size has been shown in many species and could be demonstrated by field experiments, in which the presence of predators or food availability, for example, could be manipulated.

Moreover, the type of groups found is affected by the ability of males to monopolize females. Here, different factors play a role in the sense that, the more synchronous food productivity becomes, the more females will come into estrus simultaneously. At the same time, this makes it more difficult for the males to monopolize the females against male rivals. In other words, food production patterns can directly affect the number of sexually active females, which in turn influences the number of males and the group structure (one-male versus multimale groups). In addition, in primates, infanticide by adult males has been proposed to play an important role in influencing long-term associations between females and males; the higher the risk of infanticide, the more important such affiliations are to females because males will protect their infants from infanticidal males (Palombit, 1999; van Schaik, 1996; van Schaik & Kappeler, 1997). It is important to note here that limiting infanticide risk can be complementary to predator avoidance, because both can be improved by having more individuals in a group; however, infanticide risks should be further improved if females associate permanently with the fathers of their offspring (van Schaik, 1996).

Many primate species live in groups. Thanks to the increasing number of studies on different populations within the same species, group size has proven to be highly variable and predominantly affected by the different ecological conditions each population encounters. For example, Hanuman langurs (*Semnopithecus entellus*) have been studied in many sites throughout the Indian subcontinent, and it has been shown that one-male groups predominate in environments with high food availability, high visibility, and with the number of females that can be monopolized by one male, whereas multimale groups were observed more regularly in environments with more and more predictable food, lower visibility, more predators, and larger numbers of females (review in Koenig & Borries, 2001). Such differences in group patterns were shown to have a direct impact on the reproductive success of both males and females, because infanticide is much more frequent in one-male groups. Baboons living in many parts of the African continent have been shown to adapt their group size in similar ways. The classic example is the Hamadryas baboons (*Papio hamadryas hamadryas*), which are found only in the dry regions of Ethiopia and the Arabic peninsula. They possess a rigid one-male grouping pattern, but add to that a flexible fission-fusion layer by which one-male groups can associate in larger clans, which form temporary bands and gather as large troops at rare but predator-safe sleeping cliffs (Kummer, 1968; Schreier & Swedell, 2009). In habitats rich in palm fruits, both bands and clans are larger and contain more one-male groups than other regions.

Chimpanzees (*Pan troglodytes*) seem to follow a similar pattern, because populations facing both higher predation pressure and more food availability live in larger parties, which is a name given to temporary associations of individual members from the same community, the stable grouping unit in that species (Anderson Nordheim, Boesch, & Moermond, 2002; Boesch, 2009; Mitani, Watts, & Lwanga, 2002). In some populations, food availability is a direct predictor of party size, whereas in others, sexual opportunities, in terms of the number of estrus females present, will more directly influence party size. However, females, who are more dependent on food for breast feeding their infants, are more sensitive to food scarcity and will tend to use less of the community's home range when less food is available to them (Boesch, 2009; Langergraber, Mitani, & Vigilant, 2009; Williams, Pusey, Carlis, Farm, & Goodall, 2002). The contrast in female social position is large between the more solitary and narrower-ranging females from Gombe National Park and the highly social and wide-ranging ones from Taï National Park. However, recent observations of the social behavior of female chimpanzees at Ngogo and Goualougo indicate that females can be even more flexible. What seems to be emerging is a species that is very flexible and presents both flexible party size and flexible sex-specific responses to local conditions.

The importance of ecological factors in explaining the specificity of the social grouping parameters observed in different primate species is in line with the biological knowledge we have of those species where not only the behavior but also morphology and physiology reflect an adaptation to living conditions. However, social behavior is not limited to only social grouping patterns, and we should expect many different aspects of social behavior to be precise adaptations to a group's living conditions. I will now review some evidence obtained from observations of wild populations of primates, which illustrates how complex and subtle the influence of the environment can be in promoting different aspects of social behavior, such as cooperation and altruism.

Evolution of Cooperation

Cooperation has been defined as the joint action of two or more individuals to achieve or attempt to achieve a common goal that would be more rarely achieved by an individual alone (Axelrod & Hamilton, 1981; de Waal, 2008; Dugatkin, 1997; Hamilton, 1964; Hauser, McAuliffe & Blake, 2009; Krebs & Davis, 1991; Maynard-Smith, 1982; Packer & Ruttan, 1988) (see Box 26.1). Such interactions have also been called "mutualist" or "mutual benefit." Some have expanded cooperation to encompass any social interactions in which the receiver obtains a benefit from the actor, which would then include altruism (Clutton-Brock, 2009; Fehr & Gächter, 2002; Henrich & Henrich, 2006; McNamara, Barta, Fromhage, & Houston, 2008; West, Griffin, & Gardiner, 2007). There are strong reasons to maintain a distinction between the terms *altruism* and *cooperation,* because the outcomes of the two are quite distinctive for the two partners and, therefore, they represent two distinctive evolutionary challenges (see later). Cooperation, as defined earlier, has been observed in many animal species and in many different contexts. These contexts range from group hunting, as seen in Harris hawks, some fish, hunting dogs, lions, hyenas, and chimpanzees, to group defense against predators or neighbors, as seen in many species of birds, carnivores, and primates (e.g., Boesch 2002, 2009; Bshary, Grutter, Willener, & Leimar, 2008; Dugatkin, 1997; Packer & Ruttan, 1988; Raihani, Grutter, & Bshary, 2010). In as much as cooperation is successful and leads to higher benefits to the participants than would try to attain a goal alone, the evolution of cooperation is easy to understand (Dugatkin, 1997; Maynard-Smith, 1982; West et al., 2007). However, it has proven more difficult to document the effective benefit increase resulting from cooperative actions, as the net benefit of any actions in the wild is dependent on the specific ecological conditions encountered when individuals cooperate. For example, hunting success will be strongly influenced by the availability of prey, and the ease with which prey can be subdued, as well as how detectable both the prey and hunters are (Boesch & Boesch, 1989; Packer & Ruttan, 1988). Within the same species, this can result in hunters being very successful when hunting alone under some ecological conditions, unsuccessful under other ecological conditions, or only being successful if hunting in a team.

Box 26.1 Terminology about cooperation and altruism

This table shows the cost and benefit outcomes of four main social interactions generally distinguished in the social domain: Cooperation is when both partners profit from an interaction, Selfish is when the actor gains but the recipient loses, Altruism is when the actor loses but the recipient gains, and Spite is when both partners incur costs (e.g., Axelrod & Hamilton, 1981; Hamilton, 1964; Maynard-Smith, 1982; Trivers, 1971, 1985).

	Actor	Recipient
Cooperation	+	+
Altruism	–	+
Selfish	+	–
Spite	–	–

This original classification, proposed by Hamilton, was followed for a long time, despite difficulties with measuring costs and benefits in the wild. Recently, some economists and anthropologists have started to use the term *cooperation* interchangeably with *altruism,* which suggests that the important aspect is the recipient side of the interactions (e.g., Bowles, Choi & Hopfensitz, 2003; Boyd, Gintis, Bowles & Richerson, 2003; Fehr & Gächter, 2002). Furthermore, as an altruistic act could be reciprocated by the recipient at a later time, if one counts the cost/benefit for such longer time periods, the outcome will resemble that of cooperation. Thereafter, it was suggested to reserve the terms *mutualism, mutually beneficial cooperation,* and *direct cooperation* to *cooperation* as defined in the table above (e.g., Wells et al. 2007). Others have started to talk about "costly cooperation" or "altruistic cooperation" when they intended to mean "altruism" as in the table above (e.g., West et al. 2007). Distinguishing the two terms, however, is important because in evolutionary terms, the evolution of cooperation has been quite directly explained, while the evolution of altruism remains a puzzle.

African lions provide a perfect illustration of such a situation: they were originally proposed to be a good example of successful cooperators from a limited set of observations; George Schaller (1972) showed that pairs of lions in the Serengeti in Tanzania are more successful than lone hunters at hunting Thompson gazelles. For a long time, this remained a textbook example of the benefits of cooperation. However, a more recent and extensive study of lions within the same habitat showed that lions would be more successful when hunting alone or in large groups, but that they are mainly seen to hunt in middle-sized groups (Packer, Scheel, & Pusey, 1990). However, with increasing studies of different lion populations, the situation became more complex; in Chobe National Park, Botswana, lions hunt more systematically in groups in order to defend their kills when competing with the powerful hyenas (Cooper, 1991), as do lions in Etosha National Park, Namibia, where living in an open, high visibility, semi-arid environment requires group coordination for hunting to be successful (Stander, 1992; Stander & Albon, 1993). The lion example perfectly illustrates how careful we need to be when discussing the evolution of cooperation, because, within the same species, different ecological factors may select for different levels of cooperation. In addition, when lions work in teams, as in Namibia, individual hunters monitor the actions of the other hunters so as to make the success of the joint goal possible—for example, drivers push prey toward where the other lions are ambushed (Stander & Albon, 1993).

The best example of a hunting primate is the chimpanzee. In all chimpanzee populations studied today with enough detail, males have been seen to hunt monkeys, duikers, and bushpigs for meat (Boesch & Boesch-Achermann, 2000; Boesch, 2009; Goodall, 1986; Mitani & Watts, 2001; Mitani et al., 2002; Mitani, 2009b; Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992). In all those populations, chimpanzees have been seen to hunt in groups and, when successful, they have been seen to share the meat in one way or another with group members (Boesch & Boesch-Achermann, 2000; Gilby, Eberly, Pintea & Pusey, 2006; Nishida et al., 1992). However, they are not the only primate species that have been seen to hunt. The olive baboons of Gilgil in Kenya were famous for being the only baboon population seen to hunt young antelopes for meat (Strum, 1981). However, the hunt was performed solely by the dominant male, and meat was passively shared with other individuals, who he tolerated to recover meat scraps that had fallen on the ground. Once this dominant male lost his position to a younger male, the newcomer started to forcefully steal the meat from the old dominant male who, thereafter, rapidly stopped hunting. As a result, hunting disappeared from this group (Strum, 1981). This shows that, besides ecological factors, we need to consider that social factors also affect the presence of cooperation.

The most striking aspect of hunting in chimpanzees is that group hunting tendencies diverge strongly among different populations (see Figure 26.2a) and that, when hunting in groups, the organization within the hunters differs strongly between populations (see Figure 26.2b) (Boesch, 1994, 2009; Boesch & Boesch-Achermann, 2000; Gilby et al., 2006; Gilby, Eberly, & Wrangham, 2008; Goodall, 1986; Nishida et al., 1992; Watts & Mitani, 2002). In fact, Taï and Ngogo chimpanzees were observed to hunt mostly in groups, whereas Gombe and Mahale chimpanzees primarily hunted solitarily. The level of coordination between hunters during a group hunt seems to differ, too, with Gombe and Mahale male chimpanzees hunting independently but at the same time on the same group of prey, whereas Taï male chimpanzees coordinate their actions by predominantly performing complementary and different hunting roles. The Ngogo chimpanzees live in

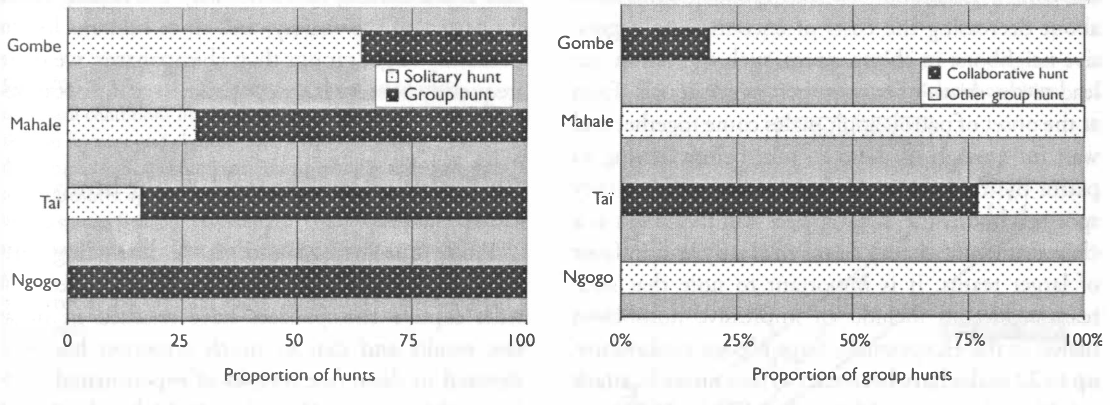

Figure 26.2. Comparison of the level of group hunt (a) and cooperation (b), in the sense of the level of coordination between hunters acting at the same time (sensu Boesch and Boesch 1989) among the chimpanzees of Gombe Stream and Mahale Mountains National Parks, Tanzania, Taï National Park, Côte d'Ivoire, and Ngogo in Kibale National Park, Uganda.

a much larger community, and up to 25 males can hunt at the same time, which makes it difficult to determine the level of coordination between hunters (Watts & Mitani, 2002).

What is also fascinating is that male chimpanzees belonging to different populations share prey meat according to different social rules (Boesch 1994, 2002, 2009; Gilby 2006; Goodall, 1986; Mitani, 2009b; Mitani & Watts, 2001; Nishida et al., 1992). The Taï chimpanzee males share meat primarily according to the contribution each individual male has made during the hunt, so that hunters get more meat than nonhunters, and those who perform more important hunting roles receive more meat than other hunters. This meat-sharing rule clearly supports cooperators. The Gombe chimpanzee males, on the other hand, seem to give in to pressure from harassing beggars so that meat sharing seemed to be forced upon the meat owners; beggars are seen to prevent meat owners from eating by either covering their mouths or pulling the piece of meat away from the meat owners, behavior patterns never seen during meat-eating sessions in Taï chimpanzees. Finally, Ngogo and Mahale chimpanzee males seem to use meat as a "political currency," and they share meat preferentially with their social allies. Thus, in chimpanzees, cooperation in the context of hunting is embedded in a series of different social patterns that contribute to whether the cooperative action is beneficial or not.

Team work has also been systematically observed during territory defense in chimpanzees (Boesch, 2009; Boesch & Boesch-Achermann, 2000; Boesch et al., 2008; Goodall et al., 1979; Goodall, 1986; Watts & Mitani, 2001; Watts, Muller, Amsler, Mbabazi & Mitani, 2006). This situation is somehow different than hunting, because cooperation in this context is less about increasing benefits and more about decreasing the costs of encountering aggressive neighbors; in chimpanzees, such aggression can lead to the death of outnumbered individuals. Even at the onset of patrol, adult males come together and wait for enough of them to join before leaving to patrol the boundaries of their territory. Once they spot neighbors, the chimpanzees will face them as a close team, and victory seems to clearly lean in favor of larger teams. It is important to note that such team work can include an impressive number of males; in the exceptionally large Ngogo community, up to 27 males have been seen to join forces to attack neighbors (average = 14.6 males) (Watts & Mitani, 2001). Thus, depending on the demographic conditions, team work can reach impressive dimensions in chimpanzees. Although such team work in territorial encounters has been observed in all chimpanzee populations, support help for outnumbered individuals seems to vary according to population: Taï chimpanzees were seen to support group members in 30 percent of intergroup encounters, but it seems to be much rarer in other chimpanzee populations (Boesch et al., 2008).

A third context in which cooperation has been systematically observed in chimpanzees is when they face predators, such as leopards (Boesch 1991, 2009). In the tropical rainforests of Africa, leopard density is quite high, with seven to ten individuals per 10 km2. Direct observations have revealed that Taï chimpanzees are regularly attacked, injured, and killed by leopards, and during a five-year period, an individual risks an attack every third year (Boesch, 1991; Boesch, 2009). Following a typical prey-predator arms race, Taï chimpanzees try to decrease the costs associated with predation by cooperatively chasing leopards away each time they notice their presence, as well as countering them whenever they have attacked a group member. Here again, support is provided systematically and very rapidly to attacked group members, and this has been seen to save the lives of the attacked individuals (Boesch, 2009).

Naturalistic observations with primates show that cooperation is observed in many contexts and has some important consequences for the social life of the individuals. It is not so much the existence of cooperation with unrelated individuals that contrasts chimpanzees from humans, as has often been proposed, but rather the fact that cooperation can involve larger numbers of individuals to an extent rarely, if ever, seen in other primate species. However, in both chimpanzees and humans, this seems directly influenced by the demographic properties of the society; and since humans live in decidedly larger groups than chimpanzees, we more frequently observe large cooperative groups of unrelated individuals in humans.

An Evolutionary Approach to the Study of Cooperation

From this background, it is intriguing that so many experimental studies on cooperation with captive chimpanzees have resulted in negative results and that so much attention has been devoted to them (see reviews of experimental studies on this topic in Warneken & Melis, chapter 21 of this volume, Tomasello et al., 2005). The main point to remember when trying to make sense out of the sometimes very contradictory results that have emerged from experimental captive studies in comparison with naturalistic observations is that animals adapt to the specific socio-ecological conditions they face in nature and will be selected to use some behavioral patterns only if the conditions experienced favor them (see Figure 26.2). In other words, cooperation will be observed only if the conditions are such that teamwork pays off. Therefore, to understand this, we must first turn toward the conditions in the wild, because only animals can tell us what those favorable socio-ecological conditions can be.

Some have argued that only experimental captive studies can provide answers about the proximate mechanisms explaining the factors underlying some cognitive abilities, such as those necessary to cooperate or help (Galef, 1990; Heyes, 1993; Povinelli, 2000; Tomasello & Call, 1997). Notwithstanding, the general consensus is that "fieldwork is primary. It tells us what animals do; it sets the problem" (Tomasello & Call 2008, p. 451). Therefore, we could have expected that experimental settings would have presented problems similar to those that, in the wild, elicited the behavior or ability under study. Sadly, this seems not to have been the priority of the majority of experimental studies. However, "laboratory experiments can illuminate a species' abilities only if their results can be placed within the context of an animal's natural social behavior. In the absence of such grounding, they remain difficult, if not impossible, to interpret" (Cheney & Seyfarth, 2007, p. 26). The results of experiments may simply be artifacts of experimental procedures used, which may tell us rather little about natural abilities.

In humans, it has now been shown that subjects respond quite differently to experimental conditions compared to real life situations, and, as a rule, human subjects tend to show much more willingness to cooperate or help in artificial laboratory conditions than in real life (see Bradsley, 2008; Lesorogol, 2007; Levitt & List, 2008; List, 2006, 2007). In addition, by manipulating experimental procedures, it is possible to dramatically influence the tendency to share in humans from different cultural backgrounds. Therefore, as in the economic sciences, one of the greatest challenges of captive psychological studies is to demonstrate its applicability in the real world (see Allen, 2002; Bekoff & Allen, 1997; Boesch, 2007, 2008; de Waal 2001)

The general and often uncritical acceptance of experimental studies with primates seems to rest on an unformulated Cartesian assumption (Penn et al., 2008; Penn & Povinelli, 2007; Tomasello et al., 2005), whereby the role of the environmental conditions on the cognitive development of individuals is considered to be minimal (see Figure 26.2). Cooperation in wild chimpanzees, as we saw, concentrates on some specific ecological situations, like hunting, and predator and territorial defense, which are not present in captive conditions. Ideally, experimental studies should measure the ability for cooperation in chimpanzees in those three specific contexts. However, this has never been done. Obviously duplicating or mimicking such situations in captivity is far from simple, but at the least, this strong limitation in the "ecological validity" of any captive study of cooperation should be addressed. The low level of cooperation found in captive chimpanzees might simply reflect the impossibility of providing ecologically valid situations in such settings, as well as the difficulties of mimicking conditions that might, from the chimpanzee's point of view, require cooperation (Boesch, 2007, 2010; de Waal, 2001). Recently, higher consideration for the social dimension of cooperation has led to better performance

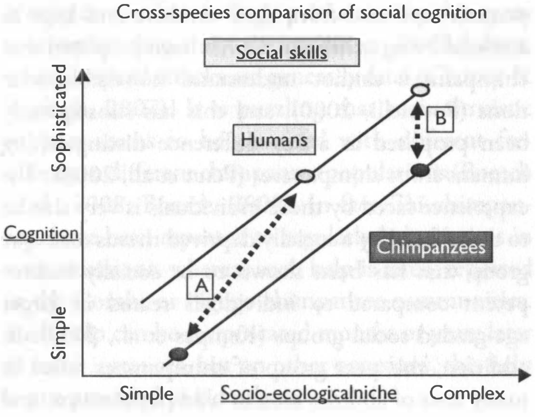

Figure 26.3 Schematic illustration of the effect of socio-ecological conditions on the development of social cognitive skills in humans and chimpanzees, two species living in very different ecological conditions. The arrows illustrate two types of comparative approaches: the first (A) compares populations of two species living in very different socio-ecological conditions as is too often done with captive chimpanzee studies, and the second (B) shows a preferable comparison, one between species living under comparable socio-ecological conditions.

by subjects in captive experimental settings (Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006). It remains that providing individuals with constant and overabundant food in human-planned social groups with no life-threatening challenges may be far from ideal for mimicking the socio-ecological situations under which we see chimpanzees cooperate in the wild (see Figure 26.3). "Ecological validity" in captive conditions is a central limitation and makes the use of captive studies very unsatisfying for studying such complex social behavior as cooperation, altruism, and reciprocity.

Evolutionary theory predicts that cognitive abilities will be shaped by the daily challenges encountered during the life of an individual, in that the more challenging the situation is, the more sophisticated the cognitive solutions will be (Barrett et al., 2007; Boesch, 2007, 2010; Cheney & Seyfarth, 1990, 2007; de Waal, 2001) (see Figure 26.3). Therefore, in all animal species, including humans, we should expect to see different levels of cognitive performances, the more diverse the ecological conditions faced by different populations in those species. Extensive differences in folk psychology, cooperation, altruism, and logic have been documented in different human societies living under very diverse ecological and economic conditions (Atran, Medin, & Ross, 2005; Henrich et al., 2005, 2006, 2010; Marlowe et al., 2008; Nisbett & Miyamoto, 2005). Whenever we make comparisons between species, it is essential that we consider this aspect and limit our comparisons to populations facing similar socio-ecological challenges (see Figure 26.3, where comparison B should be privileged over comparison A) (Boesch, 2007, 2010). If we do not do this, there is no way we can determine if the differences we observe are due to differences between the two species or differences within one species due to different socio-ecological conditions. For example, from studies done with a very small peer group of chimpanzees separated from their mothers and kept in artificial living conditions, it has been proposed that chimpanzees cannot understand nonvisible relations (Povinelli, 2000), and this has subsequently been proposed as a key difference distinguishing humans from chimpanzees (Penn et al., 2008). The experience faced by those individuals is very similar to those faced by a socially deprived rhesus macaque group that has been shown to be socially incompetent compared to individuals reared in larger age-graded social groups (Kempes et al., 2009). In addition, this peer group of chimpanzees failed in many tests of abilities seen in wild populations, and abilities that have been successfully solved by other captive chimpanzees living in larger age-graded groups. Therefore, this limitation may reflect a difference in the upbringing conditions experienced by these individuals and not a species-specific limitation (Allen, 2002; Boesch, 2010). The discussion about the influence of methods used during experiments is still very much in its infancy in comparative psychology (see Barth, Reaux & Povinelli, 2005; de Waal & Ferrari, 2010).

Recently, a shift has been proposed in some of the psychological literature stating that it is not the mere fact of cooperating that is suggested to be unique to humans but more the precise motivation underlying such an action. Human cooperation is rooted in a general tendency toward shared goals and intentions, whereas animal cooperation is a purely individualistic optimizing act (Moll & Tomasello, 2007; Tomasello et al., 2005). Detailed observations of cooperative hunting behavior in chimpanzees completely contradict such claims (see Boesch, 2002, 2005, 2010), because the performance of some hunting roles, like driving the prey, are not compatible with an individual optimization interpretation; such roles rarely lead to a capture, and the amount of meat received by the hunters is relatively low. The more general issue when stating a difference in motivation is that such a proposition is basically not testable with nonspeaking animal species in natural conditions, and as such, it is more an act of faith than a scientific hypothesis. In addition, when the proponents of such ideas tend to deny the conclusive value of data collected from naturalistic observations (see Povinelli 2000; Penn et al., 2008; Tomasello & Call, 1997; Tomasello et al., 2005), the discussion is not a matter of scientific enquiry but of intellectual preference.

Evolution of Altruism

Altruism has been defined as a costly act that one individual provides to another individual, who directly benefits from it (see Box 26.1; Axelrod & Hamilton, 1981; de Waal, 2008; Hamilton, 1964; Krebs & Davies, 1991; Maynard-Smith, 1982; Trivers, 1971; West & Gardner, 2010). As such, altruism is a puzzle because it is not expected to occur under an evolutionary framework in which individuals are expected to be selfish and to invest only when it is beneficial to themselves. However, many behavioral patterns that have been seen in animals look as if they are altruistic, such as the numerous instances of food sharing seen in many animal species, instances of helping injured or needy individuals, and adoptions. Two main evolutionary mechanisms have been proposed to explain the evolution of altruism. The first is kin selection, whereby individuals would behave altruistically only to closely related individuals and so would indirectly benefit themselves (Hamilton, 1964). The second mechanism that would lead to the evolution of altruism is reciprocal altruism between unrelated individuals, by which individuals would reciprocate altruistic acts preferentially toward individuals who have been altruistic with them (Axelrod & Hamilton, 1981; Trivers, 1971).

Because altruism between genetically related individuals indirectly contributes to the inclusive fitness of the individual, it is altruism between nonrelated individuals that has drawn more attention. As seen in primates, reciprocal altruism will work in small stable social groups in which individuals always have certain likelihoods of interacting with one another in the future. In very large and anonymous groups, as seen in some human societies and many insect and bird species, this is less certain, and the evolution of altruism is more difficult to understand. However, it has been shown that individuals within groups do not interact with others at random but tend to bias their interactions toward a limited number of group members, and, as confirmed in models, this would then make the evolution of altruism much more likely (Barrett, Gaynor, & Henri, 2002; de Waal, 2008; Nowak, 2006).

To confirm this, sharing and helping are two forms of altruism that have been regularly observed in wild chimpanzee populations as well as other primate species (Boesch et al., 2008, 2010; de Waal, 2001, 2008; Mitani et al., 2002). Furthermore, in chimpanzees, meat sharing between unrelated adult males happens in all populations and the sharing rules are influenced by the social properties of the population. This suggests that specific benefits are pursued by the meat owner. However, meat is shared with many more individuals than only the male hunters or his allies, and in many of these instances, they include nonrelated individuals. In addition, meat is spontaneously and actively offered by meat owners to other group members (e.g., in Taï chimpanzees, up to 7 percent of all meat transferred is actively given to bystanders by the meat owner and 32 percent of the meat access is actively facilitated by the meat owner; Boesch & Boesch, 1989).

Altruism in the form of adoptions of orphans by adult group members has been seen in many primate species for different lengths of time. Adoption is a very costly behavior because it involves carrying, suckling, protecting, and caring for the foster infant for many months (Boesch, Bolé, Eckhardt & Boesch, 2010; Goodall, 1986; Riedman, 1982; Thierry & Anderson, 1987). In many instances, the adoption is performed by related group members, mostly siblings of the orphans, but they are also performed by unrelated group members. In chimpanzees, adoption has been seen regularly and since orphans younger than five years of age do not survive, adoption is hugely important to them. In Taï chimpanzees, half the orphans are adopted and males do half these adoptions (Boesch et al., 2010). Specifically, adult males have been seen to adopt orphan males and females that they are not related to, and some of these adoptions lasted for years. Skeptics of altruism in animals have suggested that adoption could be attributed to errors, whereby the males would mistakenly view the orphan as his own offspring, but this argument certainly does not hold up with adoptions by adult females, who perform 50 percent of the adoptions in the Taï chimpanzees. An additional contradiction comes from the fact that chimpanzee males seem to recognize their own offspring (Lehmann, Fickenscher, & Boesch, 2006).

In chimpanzees, some of the altruistic behaviors suggest that they have a notion of the needs of others, and that they are willing to take a great deal of risk to help others (e.g., Boesch, 2009; de Waal, 2008). Altruism in the form of risky help is regularly seen, as was already mentioned, toward individuals in difficult situations, such as during predator attacks or intergroup encounters (Boesch, 2009; Boesch & Boesch-Achermann, 2000). It is important to note that leopard or chimpanzee attacks are not immediately fatal and, therefore, there is always a time window in which individuals can successfully rescue the victim. This may explain why such help is seen more often in large primates, like chimpanzees, rather than in smaller primates, like baboons, where leopard attacks are generally fatal (Cheney & Seyfarth, 2007). It is puzzling that such altruistic support seems to be provided with different frequency in different chimpanzee populations (Boesch et al., 2008; Boesch, 2009). In fact, Taï chimpanzees have been reported to regularly help victims in such situations, whereas such help is rarely reported in the Gombe or Ngogo chimpanzee communities. Such help can be reciprocated months or years later in some instances, but on other occasions, this help is just provided to aid others.

An Evolutionary Approach to the Study of Altruism

Some have proposed that altruistic acts toward unrelated group members are unique to humans and are an essential characteristic of human sociality (Fehr & Fischbacher, 2003; Fehr & Gächter, 2002; Hrdy, 2009; Silk et al., 2005; Vonk et al., 2008; Warneken, Hare, Melis, Hanus, & Tomasello, 2007). Luckily, *Homo sapiens* is the most studied of all animal species and, because altruism is considered a topic of central importance, we have access to a great many studies to help us qualify such a strong claim.

First, detailed experimental studies have now been performed in many different human societies, and the tendency to share has been observed in all of them (Henrich et al., 2006, 2010; Gintis, Bowles, Boyd & Fehr, 2003). However, the tendency to share is dramatically different in different human societies. For example, the way western university students share, which has formed the basis for the preceding claim, has been shown to be nonrepresentative of humans, who generally share much less and are reluctant to punish those who do not share. In humans, sharing and altruistic punishment have been shown to decrease in smaller human societies (Marlowe et al., 2008) and are less frequent in less socioeconomically developed societies (Gintis et al., 2003; Henrich et al., 2010).

Second, many economists have been concerned about the "ecological validity" of the experimental work, and they have carefully looked at both the effects on the subjects of the procedures used during experiments and at the differences in reactions between individuals tested in the laboratory and those tested in the real world (see review e.g., Levitt and List, 2007, 2008). Such comparisons have revealed that humans react differently in the laboratory (subjects tend to be more generous than in real life) and that very different results can be obtained according to the procedures used during the experiment.

> We believe that several features of the laboratory setting need to be carefully considered before generalizing results from experiments that measure pro-social behaviors to market settings they purport to describe... Such factors include both the representativeness of the situation as well as the representativeness of the population: the nature and extent of scrutiny, the emphasis on the process by which decisions are made, the artificial limits placed on the action space, the imposition of task, the selection rules into the environments, and the stakes typically at risk. In contrast to the lab, many real-world markets operate in ways that make pro-social behavior much less likely... Because the lab systematically differs from most naturally occurring environments on these dimensions, experiments may not always yield results that are readily generalizable. (Levitt & List, 2007, p. 168–169)

They concluded that "[p]erhaps the greatest challenge of behavioural economists is demonstrating its (the laboratory's) applicability in the real world" (Levitt & List, 2008, p. 909), and that "the data suggest that current interpretations of dictator game data likely need revision. Rather than representing social preferences as currently modeled in the oft-cited literature, the data are consistent with the power of changing the giver and recipient expectations" (List 2007, p. 490). For example, the prosocial or altruistic tendency in humans was extensively documented in numerous studies using the Dictator game. Such a game, in which the dictator receives a lump sum of money and can give as much as he wants to a receiver who cannot retaliate even when he gets nothing, has been used in many situations; humans tend to always give something. This has been used to support claims of a universal human tendency to care for the welfare of others. However, the difficulties any charitable organization encounters in collecting enough donations for their activities show that this conclusion is totally unrealistic. More precise studies have shown that this conclusion holds only as long as the dictator knows that the receiver is expecting something. In contrast, if the receiver is not aware a game is taking place, the dictator is willing to exit the game without giving anything to the receiver in almost 50 percent of the cases (Dana, Cain, & Dawes, 2006). Such studies have shown that giving does not necessarily reflect a prosocial tendency but instead might be strongly affected by the expectations of others (see also Bradsley, 2008; Henrich et al., 2010 for similar conclusions). Recognizing the specific effects laboratory experiments have on subjects is essential if we want to understand the natural social behaviors of human and nonhuman primates.

From this perspective, it is intriguing that experimental psychologists have so rarely questioned the "ecological validity" of their captive experiments. Studies on altruism and helping with captive chimpanzees have resulted in negative or mixed results (see review, chapter 20 of this volume, and e.g., Brosnan et al., 2009; Jensen, Call & Tomasello, 2007; Silk et al., 2005; Vonk et al., 2008; Warneken & Tomasello, 2006; Yamamoto & Tanaka, 2010). From these, comparative psychologists have suggested that altruism, in the form of sharing and helping, can sometimes be found in captive experimental situations, but that chimpanzees have limited interest in doing so, either because food sharing is very difficult for them (Jensen et al., 2007; Warneken & Tomasello, 2006), or because sharing does not come spontaneously but will follow from a request from a partner (Yamamoto & Tanaka, 2010), or because they are indifferent to the welfare of others (Silk et al., 2005). The contradictory outcomes of such experiments, however, suggest an intrinsic problem with the methods used, as has been shown in humans; captive chimpanzee seems to be reacting to the specific procedures used for each of the different experimental settings used with them, rather than reacting to a specific "sharing with other tendency" (see also a very recent result confirming this by Horner et al., 2011).

Evolution of Reciprocity

In stable social primate groups, group members can potentially interact over many years, and, therefore, there are plenty of opportunities to reciprocate aggressive or affiliative interactions. Repeated social interactions would increase the efficiency of cooperative and altruistic interactions because they would make it possible to distinguish between potential partners in terms of quality and reliability and, therefore, limit the problem of cheaters. Such a benefit would be especially important in animal species that maintain long-term associations between certain group members, as has been shown in some primate species (e.g., Lehmann & Boesch, 2005; Mitani, 2009a; Silk, Alberts & Altmann, 2006b). This, in turn, could increase the survival and reproductive success of individuals (Silk, Alberts, & Altmann, 2006a).

When a researcher is faced with this large potential advantage to long-term social reciprocity, it is puzzling how hard it was to find conclusive evidence of reciprocity in primate species (see Barrett et al., 2002; Gomes, Mundry & Boesch, 2009; Hauser, 2006). In some species, only evidence of short-term reciprocity could be found; for others, nothing; and for a few, some long-term reciprocity. However, in many cases, alternatives to reciprocity have been forwarded. Following this, it has been proposed that reciprocity in animals must be rare because it is too demanding (Stevens & Hauser, 2004). In particular, temporal discounting, numerical discounting, and memory would make reciprocity difficult for animals. However, more thorough reviews of the evidence support the fact that reciprocity plays an important role in grooming exchange in primates, a result that is explained as resulting from simpler cognitive mechanisms (Schino & Aureli, 2010).

A detailed study in Taï chimpanzees illustrates the question of reciprocity in primates; the symmetry of grooming exchanges within dyads increases as longer time windows are considered (up to 15 months) and reaches more than 83 percent (Gomes et al., 2009). Because grooming interactions in the fluid social system of chimpanzees were observed only between the same dyads every seventh day (range = 2 to 18 days), such levels of reciprocity can only be achieved with some means of keeping track of past interactions. Besides grooming interactions, Taï chimpanzees trade meat for sex as well as meat for support with all adult group members, and they also reciprocate support interactions (Gomes & Boesch, 2011). Two proximate mechanisms have been proposed for individuals to keep track of past interactions: "emotionally mediated" scorekeeping and calculated reciprocity (de Waal & Luttrell, 1988; Schino & Aureli, 2009). The first is based on the emotional attitude that develops between partners as a consequence of prior affiliative or aggressive interactions. Calculated reciprocity, on the other hand, requires a detailed cognitive accounting of the amount of services given and received. When distinguishing between these two mechanisms, it is important to remember that the amount of grooming and support interchanged as well as the trading of meat and support varied dramatically within and between dyads, requiring that an emotion-based scorekeeping be sufficiently structured so that it would allow each individual to precisely differentiate and update among 43 to 52 adult dyadic interactions. Such structured emotion-based scorekeeping would possibly be very similar to full blown calculated reciprocity.

Discussion

The present review of social behaviors and cognitive abilities in primates supports the evolutionary approach by showing the key importance of the socio-ecological challenges on the behavioral solutions adopted by the individuals. Convergent evolution of similar social behavior and cognitive solutions have been seen in such diverse species as crows, ravens, scrub jays, dogs, fish, baboons, rhesus monkeys, chimpanzees, and humans (Boesch, 2007; Cheney & Seyfarth, 2007; Bshary et al., 2008; de Waal, 2008; de Waal & Ferrari, 2010; Fitch et al., 2010). Similarly, in species living in different ecological challenges, we observed the adoption of large numbers of different behavioral and cognitive solutions, and this effect was more pronounced in more adaptive species (Boesch, 2007, 2009; Henrich et al., 2010). Such observations are not compatible with a Cartesian approach to the evolution of social behavior and cognition, and have often been simply ignored or dismissed as naturalistic anecdotes (Penn et al., 2008; Povinelli, 2000; Tomasello & Call, 1997; Tomasello et al., 2005).

Social interactions are adaptive responses to the specific circumstances encountered by individuals within their social groups. If circumstances change, we would expect individuals to adapt their behavior so that they make the best out of the situations they face. Long-term studies have proven to be one of the best approaches to address such issues, and they have provided many insights into the flexibility of primate social behavior patterns. For example, female chacma baboons have been shown to adapt their social interactions to variations in competition levels (Barrett et al., 2002). A similar flexible response to the ecological and social circumstances has been shown in the dispersal decisions by males in different species of baboons (Alberts & Altmann, 1995; Clarke, Henzi, Barrett & Rendall, 2008). In line with this, cooperation has been shown to be flexible and observed mainly in situations in which the individual is paid off for investing in such joint efforts. In chimpanzees, cooperation is flexibly observed when hunting arboreal monkeys, and in communal defense against predators and conspecific neighbors. Similarly, altruism is concentrated in cases when high-value food resources are shared and when recipients are provided with large benefits like support and adoptions.

Comparative studies on potential differences in social behavior and cognitive abilities have made a great deal of progress thanks to the increasing number of detailed long-term studies with different primate species, which, for the first time, have provided science with insight into "how primates see the world" (e.g., Boesch, 2009; Cheney & Seyfarth, 1990, 2007; Goodall, 1986). At the same time, the confirmation of important differences within a species has greatly complicated the task for comparative studies, because it requires a large number of populations to understand the interplay between socio-ecological influences and the expression of the different behavioral patterns. Until shown differently, at present, we can say that, in chimpanzees, cooperation is concentrated in social domains in which teamwork is mandatory for solving challenges. When the conditions vary, however, cooperation may disappear and individual solutions will be preferred. Because teamwork requires all participants to coordinate their behaviors with one another in time and space, as well as share the risks and benefits, we should expect such complex group actions to be performed only if necessary. Assuming that animal species possessing the cognitive abilities to cooperate or help should always do so ignores the costs that are associated with such social behaviors. Therefore, ecological validity is of central importance if we want to understand the evolution of social behavior.

Future Directions

The field of social cognition has been dominated by a debate about the value of captive animal experiments (e.g., Allen, 2002; Boesch, 2007, 2008; de Waal, 2001; Tomasello & Call, 1997). On one side of the debate, experiments are the only way to provide answers to cognitive questions, because this is the only way to control for all possible factors that influence individuals in their natural life (Galef, 1990; Heyes, 1993; Penn et al., 2008; Tomasello & Call, 1997). This has led some scientific disciplines, like experimental and comparative psychology, to concentrate on captive studies to the point that one has the impression that animals live only in captivity and that wild animals are outliers. To highlight this, some high-profile experimental studies on animal cognition do not cite even a single study of their study species living under natural conditions. Not surprisingly, on the other side of the debate, captive studies have been strongly criticized for having very little to no ecological validity and presenting animals with extremely artificial situations (Barrett et al., 2007; Boesch, 2007, 2010; Cheney & Seyfarth, 2006; de Waal, 2001). The fields of comparative and experimental psychology sometimes see captive studies from a Cartesian approach, by which the differences in upbringing and ecology are considered of very little relevance for understanding the performance of an animal species. However, until the impact of development and ecology is clearly integrated into our thinking, our understanding of species differences will remain totally biased and incomplete. To make some progress in solving this debate, it seems important to have more information on the following points:

1. Quantify the role of ecological differences on the development of social behavior and cognition in different primate species.

It is striking that, after over 100 years of comparative psychology, no systematic study exists on the role of captivity on the development of social behavior and cognition. The closest study was undertaken in the 1960s by Gardner and Gardner (1989) with a small sample size, by comparing only two different rearing conditions. This study clearly showed that young chimpanzees differed strongly in all possible measures. Sadly, such a pioneering study was not followed, and we are left wondering about such effects (see, however, Lyn, Russel, & Hopkins, 2010). In economic science, this has been done to the point that some argue that "behavior in the lab might be poor to real-world behavior" (Levitt & List, 2008). In a sense, this important gap in our knowledge allows psychologists to maintain dramatically different opinions. It is not that we are missing data on the dramatic consequences of strongly deprived captive conditions, as they still prevailed in the early 1950s (Harlow & Harlow, 1962), but direct comparisons with wild living animals have not been done. We saw that even relatively small deprivations can have large and long-lasting detrimental effects on an individual's development, and we are simply missing more information of the effect of this on different primate species. Only with such studies will cognitive sciences be able to scientifically evaluate the applicability of captive studies to the real world.

2. Quantify the effects of different upbringing conditions on the cognitive development of the individuals.

Upbringing has been shown to have very important and long-lasting effects in individual humans, and the field of social psychology has provided data on how poor socioeconomic conditions are detrimental to the development of social cognitive skills. Recently, more efforts have been done to quantify some of these effects in chimpanzees facing different social conditions in captive settings, and they have shown strong but specialized effects. For example, mirror recognition, often considered as a measure of self-recognition, has been shown to be strongly influenced by maternal style toward babies: more stimulation by the mothers and independent movements by the infants leads to earlier mirror recognition in both humans and chimpanzees (Bard et al., 2005; Ijzendoorn, van Bard, Bakermans-Kranenberg & Ivan, 2009; Keller et al., 2004). Such pioneering work should be replicated and applied to many other behavioral domains to see how different aspects of social cognition are affected by early experience during upbringing. The whole field of cognitive science would benefit from following the economic sciences by specifically designing studies aimed at quantifying the role of experience and design in the performance of the individual subjects.

3. Develop an understanding of the specific factors affecting the evolution of cooperation and altruism.

Cooperation, altruism, and reciprocity have become important social domains in defining potentially unique differences between humans and other primate species. However, the whole discussion is impaired by a lack of understanding of the conditions under which such behavioral patterns evolve. Most observations of cooperation and altruism have been done in natural social groups and directed toward life-long group members who solve challenges they encounter within their environments. On the other hand, most observations that found primates to be incompletely or unable to cooperate, help, or share with others were done with captive individuals facing artificial conditions (e.g., Povinelli, 2000; Tomasello et al., 2005). New experiments taking into account the social dimension of cooperation and altruism have tried to present more natural choices to the tested individuals, and they have already shown clear improvements in performance (Melis et al., 2006). More studies in this direction will allow us to gain a better understanding of the social dimension of such behavior patterns and provide an explanation of why animals tend to cooperate less and be less helpful in captive conditions than in the wild (Boesch, 2010).

4. Study nonhuman animals without anthropocentrism.

Too often, the field of comparative psychology has been guided by an anthropocentric approach, by which humans look to other animal species to explain specific human abilities (Allen, 2002; Barrett et al., 2007). Furthermore, many of these anthropocentric approaches are ethnocentric as they do not take into account that what occidental humans do is far from being representative of what all humans on this planet do (Boesch, 2007; Henrich et al., 2010). Chimpanzees, rhesus monkeys, and ravens are not humans, and, therefore, it would make more sense to ask how they solve their specific ecological and social problems. In this way, we could gain a better understanding about the evolution of abilities that are used in nature and on which our ancestors have built to produce our modern human abilities. Too often, animals are confronted with challenges that do not address their natural abilities, and the negative answers might just reflect our own inability to set ourselves in the mind of others.

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