

Chapter 7

Primates, Niche Construction, and Social Complexity: The Roles of Social Cooperation and Altruism

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The explication of altruistic behavior in primates remains complex. Gregarious, socially complex primates are characterized by a diverse array of social behavior patterns with seemingly altruistic behavior being relatively commonplace. Human societies are a form of primate society but with much higher levels of social complexity and extremely high levels of cooperative and apparently altruistic behavior. It is likely that there are elements of primate (at least anthropoid) sociality that act as baseline for subsequent expansion and elaboration during human evolution. Can understanding patterns and contexts of primate social complexity and cooperation help us understand human altruism? In this chapter we have two primary objectives: to examine three nonhuman primate genera to show how social cooperation, social bonding, and niche construction can affect our understandings of altruism and to illustrate where we think that such nonhuman primate information is a good model for humans and where it is not.

Theoretical and Historical Underpinnings

Although some argue that true altruism cannot occur (e.g., Trivers, 1971; Dugatkin, 2006), we believe it can and will use as a baseline for this chapter the assumption that it is possible that some organisms do exhibit truly altruistic behavior. However, altruism, strictly defined as acts that have a net loss of evolutionary fitness to the actor but a net gain in fitness to the receiver, does not make sense if organisms benefit by maximizing their own fitness as per basic assumptions in much current evolutionary behavioral theory. Therefore, one challenge to anyone attempting to examine altruism in a neo-Darwinian context is a theoretical justification for why it might occur. Let us briefly summarize the salient positions on this point to date.

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Darwin saw social animals as, at least partially, structurally altruistic; “impelled partly by a wish to aid members of their community in a general manner, but more commonly to perform certain definite actions” (*Descent of Man*, p. 913). Wallace saw altruistic and sympathetic behavior toward one’s fellow humans as a core adaptive pattern and competition between human groups as an essential factor in the evolution of human behavior and cognitive capabilities (Richards, 1987). Spencer noted that humans vary in their behavioral proclivities and moral senses (which he divided into selfish instinct and sentiment of sympathy). He proposed altruistic behavior as core to human evolutionary success. Spencer described two ways in which altruism could arise and become a dominant behavioral characteristic. Unlike Darwin and Wallace, Spencer saw the individual expression of altruism as having a selfish motivation. He said that as humans relate to the misery of others (engage in a sympathetic response) they act to alleviate others’ suffering in order to avoid their own (Principles of Psychology, 1855, 1872). Spencer also allowed for a form of altruism that can arise through a series of reciprocally beneficial acts between individuals and then be “selected” for if these exchanges resulted in increased fitness for the participants (The Principles of Ethics, 1893). Spencer did agree with Darwin and Wallace that within-group altruism could arise via selection. He argued that this type of altruism could arise via competition between groups, those having more altruists most likely doing better over all than those with too few altruists. In fact, he went as far as to suggest that the functional adaptation by such groups to social conditions would allow those groups to reduce the impact that challenges of the environment (natural selection) placed upon them. This perspective was even cited by the cooperation advocate Petr Kropotkin as evidence in support of his perspectives on the hyper-cooperative adaptation in humans (Richards, 1987). In short, the “founding fathers” of evolutionary theory held that altruism was a core feature of social animals, especially humans, and emerged out of either selfish intent or between-group competition. This theme has been echoed ever since, but the puzzle of a mechanism for such behavior was not elaborated by these early theoreticians.

The evolutionary biologist Lee Dugatkin wrote “Eventually biology did solve the puzzle of blood kinship and altruism in the form of a mathematical equation developed by a shy, brilliant evolutionary biologist named William D. Hamilton” (Dugatkin, 2006). This “solution” was the concept of “kin selection” and its corollary: reciprocal altruism. For many theorists these hypotheses laid to rest that the conundrum of altruism is social animals.

Kin selection, the behavioral favoring of your close genetic relatives (Hamilton, 1964), was proposed by William Hamilton to explain the dilemma posed by altruism. While Darwin, Wallace, Spencer invoked a form of group selection, natural selection acting at the level of intergroup competition, to explain why altruism occurs, the theoretical work in genetics and evolutionary theory through the middle of the 20th century produced a negative view of group selection (Williams, 1966). The focus of selection shifted solely to the individual. Kin selection offers a simple equation predicting when an individual organism might behave in a manner that looks altruistic: $r \times b > c$, with r = genetic relatedness between the actor and

receiver of the behavior, b = the fitness benefit to the receiver, and c = the fitness cost to the actor. If the individual who receives the benefit from a behavior that has fitness costs to the actor is a relative, then a certain percentage of the actor's genotype (depending on the degree of relatedness) also benefits from the action. Relatedness is then calculated as a simple percentage given a sexual reproducing system. Each offspring is assumed to share 50% of the unique genetic component of each parent, while an uncle or aunt is then related at 25% to an actor. Here genetic investment decreases as "relatives" become more distant (genotypically) from the individual. Because close kin share much of their genotype, we would expect behaviors among them to be seemingly altruistic, as they frequently appear. This simple equation, and its assumptions about genetic systems, forms an integral core to the current paradigm dominating the understanding of altruistic behavior.

Robert Trivers published "the evolution of reciprocal altruism" in 1971 drawing on ideas of Darwin, Spencer, and Hamilton, and proposing a set of mathematical models with a series of predictive assumptions which he termed "reciprocal altruism." The reciprocal altruism model states that unrelated organisms can enter into relationships that can be characterized as fitness value exchanges. Using a simplistic genetic system as a model (like Hamilton), Trivers presents a mathematical equation for the relationship between an actor and a recipient in a series of reciprocal exchanges using a prisoner's dilemma style "payoff matrix." The core of the hypothesis revolves around the frequency and symmetry of potentially altruistic situations. There are three main conditions that are relevant in the potential selection for reciprocal altruism. First, that there be many opportunities for altruistic action during the lifetime of the actors. Second, that a given actor repeatedly interacts with the same small set of individuals. And third, that pairs of altruists are exposed "symmetrically" to altruistic opportunities so that over time two such actors are able to render roughly equivalent benefits to each other while incurring roughly compatible costs. These three conditions set the stage for the selection of a reciprocal altruistic system. Some biological parameters that affect the form of the system include length of lifetime (chances of reciprocal altruism rise with longevity), dispersal pattern (low dispersal rate also favors reciprocal altruism), and degree of mutual independence (group-living animals are more reliant on one another more frequently than solitary ones). Other important biological factors include presence and type of parental care, dominance hierarchy structure, and aid in combat. Trivers predicted that if the three primary conditions are met and the biological parameters set favorable conditions, then reciprocal altruism will evolve as an adaptation in that population. This set of ideas is especially important as it had substantial influence on theoreticians since the 1970s and forms a main basis for models of animal and human behavior in many hypotheses. Recently, Trivers (2006) has argued (following deWaal and Brosnan, 2006) that nonhuman primates who practice reciprocal altruism (capuchins and chimpanzees in his example) develop a sense of aversion to inequity which can be seen as a basal sense of "fairness."

Challenging the four-decade-long aversion to group selection, Wilson and Sober (1994), Sober and Wilson (1998), and more recently Wilson and Wilson (2007), have proposed the insertion of multilevel selection as a core factor in understanding

behavior that appears altruistic (especially for humans). The basic concept is that the evolution of behavior can result from selection focusing at multiple levels: the genic, the individual, and the group. In this conceptualization extensive interaction within and between groups produces a context wherein multilevel selection can result in widespread cooperative patterns. That is, selection at the group level can favor groups that have a larger number of individuals who behave altruistically (within group) over those that have fewer such individuals. This in turn can have effects on the local gene pool shifting genotypic frequencies in accord with these intergroup, or local population, level interactions and the selective environments/landscapes they create. This allows for such behavior to emerge without having relied on either kin selection or reciprocal altruism, although both of those might also be at play within groups. A version of this perspective is also promulgated by Richerson and Boyd (2005) to explain high levels of cooperation within human groups and the concomitant competition between such groups. It is worth noting that Darwin, Wallace, Spencer, and E.O. Wilson all proposed some form of this within-group cooperation/altruism model as core to their views on human evolution (Fuentes, 2009). Many past and current theorists see these intragroup versus intergroup relationships as being major players in the augmentation of social complexity with altruistic reciprocity playing a major role for the within-group dynamics and between-group contest evolutionary success.

Thinking about the selective landscapes that such groups and populations inhabit, the concept of “niche construction” takes on particular relevance. Building on work of Richard Lewontin (1983), Ernst Mayr (1963), Conrad Waddington (1959), and taking from the “extended phenotype” concept of Richard Dawkins (1982), F. John Odling-Smee, Kevin Laland, and Marcus Feldman (2003) proposed “niche construction” as a significant evolutionary force. Niche construction is the modification by organisms of the functional relationship between themselves and their environment through an active change of one of the factors of that environment. “Through niche construction organisms not only influence the nature of their world, but also in part determine the selection pressures to which they and their descendants are exposed, and they do so in a non-random manner” (Day et al., 2003). As organisms respond to environmental selective pressures which are themselves modified by the organisms, a feedback mechanism is created, and such feedback loops can fundamentally alter the outcome of evolutionary scenarios. This mutual mutability of organism and environment is a core consideration for primate species whose primary selective environments exist as complex social networks. Flack et al. (2006) argue for a form of social niche construction in primates where social networks constitute the essential social resources in gregarious primate societies. They posit that “The structure of such networks plays a critical role in infant survivorship, emergence and spread of cooperative behavior, social learning and cultural traditions.” If this is the case and social interactions impact these networks, it could be argued that social complexity, reciprocity, and even altruistic behavior could be active agents in primate niche construction and major factors in their evolutionary trajectories (see also Fuentes et al., 2010).

Social Cooperation and Reciprocity: Can It Be Altruism?

There is little debate that strong social attachments are *necessary* for primate survival. Social bonding and the manipulation of those bonds are characteristic of all gregarious primate societies: complex sociality is a core primate adaptation (Silk, 2007). Such relationships are traditionally examined via analyses of hierarchies, cooperative alliances, and long social histories among individuals. As such, understanding social cooperation is a major element in primate studies. Cooperation can be most generally defined as social interactions that have costs to an actor and benefits to other conspecifics, and as Peter Kappeler and Carel van Schaik recently put it “Cooperative behavior is the hallmark of the primate order” (Kappeler and van Schaik, 2006).

The concepts of cooperation and altruism are closely related. However, while it is commonplace to argue that forms of social cooperation characterize many primate societies, we still have a great deal to investigate in regards to specific patterns of reciprocity and the possibility that altruism, outside of reciprocal exchanges, occurs. Reciprocity is frequently measured by analyzing coalitionary behavior, directionality/symmetry of grooming, food sharing, social association patterns, and direct cooperation in task solving. deWaal and Brosnan (2006) suggest that we can envision primate reciprocity along a continuum that ranges from Triver’s strong reciprocal altruism at one end to a reciprocity reflecting simple social symmetries at the other. They lay out three specific types of reciprocity: symmetry based, attitudinal based, and calculated. In symmetrical reciprocity, there is no “score keeping,” there is a strong mutuality of interactions, and a “strong aversion to major, lasting imbalances in incoming and outgoing benefits” (deWaal and Brosnan, 2006). One could argue that indeed, given the loose and general assessment of symmetry in exchanges, this level of reciprocity may simply be altruism as a byproduct of a social complexity that maximizes close social bonding amongst individuals within a group (between non-kin). The second level of reciprocity, attitudinal based, reflects a mild tit-for-tat strategy wherein individuals who generally have positive and predictive relationships will invest in one another without close tabs on recouping investments. deWaal and Bosnan refer to this as the “if you are nice, I will be nice” principle where the level of reciprocity is based on simple assessments of recent interactions between individuals. The final level, calculated reciprocity, is a full-blown Triver’s style reciprocal altruism which involves relatively extensive individual “score keeping” and the potential punishment of cheaters. If this continuum accurately reflects the range of reciprocity, then the possibility exists that reciprocity and altruism are behaviors that share a common origin and are differentiated by the types, contexts, and patterns of relationships between individuals. This, however, does not leave room for altruism occurring outside of familiar social partners in the nonhuman primates. Might this be a distinct difference between humans and other primates?

At this point in the discussion, it is worth briefly discussing an alternative approach to understanding cooperation: biological markets. Introduced nearly two decades ago (Noe et al., 1991), the concept of biological markets as an analytical tool has gained substantial popularity amongst primatologists (Barrett and Henzi,

2006). The basal assumptions of this paradigm match those of free market capitalist systems: (1) individuals control resources or can provide services—these are commodities that can be socially exchanged, (2) trading partners are chosen from the social context via a mechanism of outbidding competition, maximizing social profit, and (3) supply and demand determine the bartering value of the “commodities” exchanged. In other words, cooperative interactions such as coalitionary support and grooming are seen as commodities that can be traded on an open market with market forces (social contexts) driving the value of the commodities. This approach differs to an extent from the models of kin selection and reciprocal altruism in that it sees the interchange between individual variation and group contexts as creating the market driving differentiation of value in the “commodities.” This results in an expectation of a good deal of individual flexibility in behavioral response across contexts and time when cooperating (dependent on the “market” conditions at the moment of exchange). However, under this rubric, there is no category for altruism as market models inherently assume all transactions as having a value, and while actors may not try to maximize, they do try to profit. Thus transactions are a profit, a loss, or an equitable transfer, but no models including an option for “non-tax deductible charitable donation” (altruism in this system) are recognized. Our perspective on the biological market model is that it constrains analysis by limiting the types of questions one can ask and by resting on assumptions of limited good, costs, and profit taking that stem from a specific human paradigmatic world view and not necessarily the organic world.

Social and Ecological Niche Construction and Hyper-Sociality as Primate Heritage: The Social Mind, the Primate Mind and the Cultural Mind

All members of the primate order are characterized by complex interactions between their central nervous system (CNS) and the social/physical environments in which they live (sensorimotor pathways). In particular, information crucial to primate survival is disseminated primarily through *social networks*. The physiological and social correlates of this mandate are an extended period of infant development and brain maturation, which allows for the acquisition of species-appropriate skill sets and knowledge. Initiated during this period and extending for the life of the individual, primates participate in a complex practice of social niche construction (see Flack et al., 2006; Fuentes, 2009, 2011). One can envision that social complexity itself acts as a niche-constructing tool causing the interface between individuals within a group, individuals with their environment, and conspecifics groups within that local population to be seen best as a mutually mutable process. The social and biotic/abiotic ecologies are then modified by social behavior which is in turn affected by the pressures of those same social and abiotic/biotic environments.

Primates are characterized by a specific type of “social intelligence” (Dunbar and Shultz, 2007) such that “distinctive aspects of primate cognition evolved mainly in

response to the especially challenging demands of a complex social life of constant competition and cooperation with others in the social group” (Herrmann et al., 2007; Silk, 2007) in addition to the external ecological pressures. There could therefore be a ratcheting up of this social complexity in anthropoids, which is increased in hominoids and exponentially enhanced in hominins. One might envision a scenario wherein the basal complex sociality of mammals is enhanced in primates, and primates then use their social networks/contexts as a tool to meet and modify the demands of the environment (the selective landscape). As the local environments are being modified, selection pressures alter changing the selective landscapes for the primate populations. Increased cognitive complexity in the hominoids facilitates a faster or more intensive utilization of the social bonds and relationships as tools to meet ecological challenges. This increased cooperation and reciprocity becomes a central component of behavioral repertoires and is constantly engaging the social and biotic ecologies in feedback scenarios resulting in niche construction and concomitant shifting/modification of selective landscapes. As broad and complex social behavioral complexes (reliant on extensive cooperation) become commonplace in the hominins, true altruism (actions engaging in a cost for self with other’s benefit) arises as an emergent property of the system. Because of the extensive cooperation and the generally intensive reciprocity in hominins/humans, multiple instances of altruism can be experienced across the lifetimes of individuals without effectively

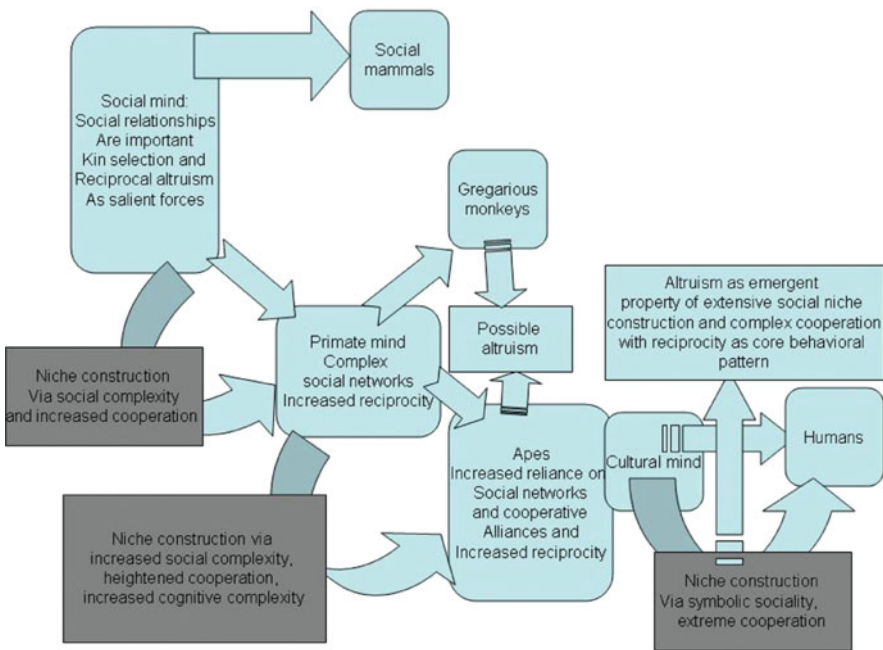


Fig. 7.1 A model for the relationship between social complexity, niche construction and the possible emergence of altruism in primates and humans

negative fitness costs. No individuals are uniformly altruistic but altruistic acts can appear, even commonly, and not be selected against within the populations. Here altruistic action emerges as a by-product of the physiological and behavioral adaptations required to effectively negotiate high level and complex social networks where coalitions, multi-party social negotiations, and reciprocity are the primary avenues for social and reproductive success (see Fig. 7.1) (see also de Waal, 1996; Hauser, 2006; Tomasello, 2009).

If this model is accurate, we should be able to look to anthropoid primates, especially those known for very complex coalitionary behavior, broad geographic range and behavioral plasticity, and see the basal components of this system. If these base-lines occur, we benefit from their study and the comparative analyses of human and other primate systems specifically in our attempts to understand the mechanisms and evolution of behavioral systems that can produce altruistic acts.

Case Studies: *Macaca*, *Cebus*, *Pan*, and *Homo*

The Genus Macaca

Macaque monkeys (members of the genus *Macaca*) are among the most widespread of any primate genus. The genus *Macaca* underwent a radiation in the Plio-Pleistocene, about 2 million years ago, similar to that of the genus *Homo* at the same time. The macaques spread across much of Asia and into central Eurasia and even northern Africa. Macaques have encountered many diverse habitats. As a result, they reflect responses to a broader range of environmental pressures than nearly any other nonhuman primate group. There are about 19 macaque species, but they tend to cluster into a few major species groups. Macaques are generalists in their feeding patterns, preferring fruit but eating a wide variety of foodstuffs, including leaves, insects, and occasionally vertebrates. They are full quadrupeds and frequently arboreal; however, most macaque species also use the ground for foraging and distance locomotion.

The majority of macaques live in multi-female/multi-male groups that can number from 10 to more than 100 individuals. There are usually more adult females than adult males in these groups, and social activity revolves around clusters of related females (Thierry, 2011). Males tend to leave their natal groups and seek out other groups to join. Females, on the other hand, are philopatric, and thus surrounded by their female relatives throughout their lives. Female macaques spend a great deal of time and energy associating and interacting with their maternal kin. A few adult males do associate with these matrifocal units, but most males are relatively solitary, remaining on the outskirts of the groups and occasionally interacting with females and other males. Subadult males may be seen together in small subgroups that have varying cohesion. An explanation for these social differences between males and females can be found in the dispersal and dominance patterns of macaque societies. Although there is a range of dominance patterns, from very strict linear (“despotic”) dominance systems to relaxed, “egalitarian” ones, macaque grouping and overall

social patterns are surprisingly cohesive but are characterized by a wider range of behavioral variation across individuals (Thierry, 2011).

For female macaques, the main arena of social interactions involves female maternal kin. Depending on the size of the overall macaque group, there are usually from two to six matrifocal units within it. The dominant matrifocal units are usually able to displace the others from prime food sources, sleeping sites, and other preferred resources. This is partly because the dominant matrifocal units are also the largest. With more individuals in a cluster, they have a better chance of intimidating or outcompeting other, smaller clusters of individuals. However, although there is strength in numbers, individuals are not always dominant on their own. Macaque females rely heavily on alliances with female relatives to gain access to resources and win competitions. There are also dominance relationships within matrifocal groups. Generally, a prime-age female (about 8–12 years old) holds the highest rank within such clusters, with youngest daughters inheriting their mother's rank.

Males have linear dominance relationships that can change rapidly. Due to their dispersal patterns, males cannot rely on kin to assist them in conflicts and need to form associations with other males and females in order to negotiate dominance disputes. High-ranked males often form coalitions with other males to acquire/defend social position and gain access to preferred resources. There are many ways for males to attain a high dominance rank. Some males are extremely aggressive and use fighting and conflict to move up the dominance hierarchy. Fighting in male macaques can result in substantial injuries; however, it is not clear how often these injuries result in deaths. Other males use association with females to form coalitions to create strong social bonds with other individuals. These males participate in much grooming and other social interactions with females and young, even including holding infants. Overall most male ranks are fragile, and males may spend anywhere from a few months to many years at high rank (Bercovitch and Huffman, 1999).

For the macaques then, kin–kin interactions and non-kin intra- and intersexual coalition formation and competition are the keystone components of their social networks. Following Flack et al. (2006), we can envision the potential for social niche construction, as individuals in macaque groups negotiate these social networks modifying their boundaries and internal landscapes in the context of changing demographic and, potentially, ecological variables. For males, the social networks need to be learned anew when moving between groups, and for females these networks are layered with intra and inter-matrifocal group relationships providing the primary social landscapes. Because nearest neighbors and most frequent interaction partners for females are often relatives, kin selection has been invoked to explain a majority of alliance and coalitionary actions by female macaques.

Adult female–adult male coalitions are rarely kin based and thus reflect possible circumstances for reciprocal altruism to occur. Such intersexual relationships could also be seen as intersexual cooperation and competition with differential payoffs to participants dependant on social skill, experience, and context. The proximate social benefits of macaque intersexual cooperation could be different for males and females. Females may receive active male assistance in dominance contests (improving their access to contested resources), while males might be receiving

social benefits such as increased grooming and social interactions. Both sexes may receive reproductive benefits and suffer reproductive costs from such alliances. Manipulation of the social networks can alter the selective landscapes (in terms of both social and reproductive parameters) changing the pressures and payoffs for all involved (social niche construction). For adult males, associations with larger or more dominant matrifocal groups might offer increased mating opportunities and an overall greater level of social interaction potentially ameliorating social stress emerging from male–male competition. However, one does see aggregations of young males who play together and spend large amounts of time in social activities such as grooming. In these cases reciprocal altruism or mutualism might be invoked to explain these social and temporally variable associations, but one could also as easily invoke a simple benefit of access to social partners. In this case, if costs are moderate or negligible in regards to overall reproductive success, we could see potentially altruistic acts emerge out of simply a high density of prosocial relationships amongst young males without any significant impact on fitness. This is also the case with large matrifocal groups wherein some females might be distantly related but extremely familiar and frequent social partners to others. In such cases, we might also expect to see possible altruism on occasion as fitness costs for such actions would be negligible, but the pattern of prosocial behavior within the whole group would be high. Obviously, we would not expect to see frequent high-cost altruistic acts in any of these cases, but one can envision in these macaque social networks many opportunities for actors to engage in small costs that benefit others with no social or physical negative repercussions.

The Genus Cebus

The genus *Cebus* traditionally consists of four species: *C. apella*, *C. albifrons*, *C. olivaceus* (formerly *C. nigrivittatus*), and *C. capucinus*, with the recently discovered *C. Kaapori* often included as a fifth species (Queiroz, 1992). There are more than 30 subspecies recognized (Ford and Hobbs, 1996). More recently, some have argued for three subspecies of *C. apella* to be listed as distinct species (e.g., Groves, 2001; Rylands et al., 2000; and see Jack, 2011 and Fragaszy et al., 2004 for reviews). All of these monkeys can be classified generally as arboreal, diurnal, medium-sized primates with robust bodies and semi-prehensile tails. The better known species are commonly divided into two morphological groups, “tufted” (*C. apella*) and “nontufted” (*C. albifrons*, *C. olivaceus*, and *C. capucinus*), based on the degree of erect hairs on either side of the crown (Hershkovitz, 1949; Napier and Napier, 1985). The primary differences between the four species are coat color, coat pattern, and geographical range (Freese and Oppenheimer, 1981). They all are somewhat similar in diet and behavior. Capuchin monkeys are found throughout Central and South America. *C. capucinus* ranges from Honduras to the northwestern part of Ecuador (Rowe, 1996) and is the only *Cebus* species that occurs in Central America. The other three species are found primarily in the Orinoco and Amazon River basins of South America and have varying levels of sympatry. *C. apella* has the most extensive range of any New World monkey and occurs throughout most of Amazonia, the

Brazilian coastal forests, and northern Argentina. On the genus level, only *Alouatta* has a more extensive range overall among Platyrrhines (Sussman, 2000).

All four capuchin species are moderately sexually dimorphic and live in large multi-male, multi-female social groups of 4–36 individuals (Freese and Oppenheimer, 1981; Fedigan and Jack, 2001). Average group sizes differ slightly: *C. capucinus* with 16.4 members, *C. albifrons* with 19.8, *C. apella* with 18, and *C. olivaceus* with 21 (Fragaszy et al., 2004). All species show linear dominance hierarchies, with an alpha male and alpha female; however, it is often difficult to determine specific individual rankings lower than beta in wild groups.

Capuchin monkeys are highly adaptable and occupy a wide array of habitat types (lowland rain forest, cloud forest, tropical dry forest, living in proximity to humans, etc). They are quite omnivorous, using a range of foods such as insects, fruits, and vertebrate prey (Chapman and Fedigan, 1990; Panger et al., 2002; Fragaszy et al., 2004). Capuchins are described as manipulative and extractive foragers: they can exploit hard-to-obtain and hard-to-process resources including larvae from embedded substrates, hard-shelled fruits and nuts, and fast-moving vertebrate prey such as squirrels, tree rats, birds, and lizards (Fedigan, 1990; Rose, 1997; Panger et al., 2002; O'Malley and Fedigan, 2005; MacKinnon, 2006). Consequently, they have been characterized as eating foods that “fight back”. The documented studies of tool/object use in *Cebus* (see Panger, 1998 for definitions, and Panger, 2007 for review; but see Garber and Brown, 2002) describe how palm nuts are repeatedly pounded against another surface until opened (Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Anderson, 1990; Visalberghi et al., 2007, 2008), how marine oysters are opened by the use of stones and other oysters (Fernandez, 1991; Parker and Gibson, 1977), and how sticks are used to groom wounds or to contact a potentially dangerous object (Boinski, 1988; Cooper and Harlow, 1961; Richie and Fragaszy, 1989; Visalberghi, 1990; Westergaard and Fragaszy, 1987). This combination of manipulative skills and an opportunistic feeding strategy allow the highly adaptive *Cebus* species to exploit different habitats and diets. Juvenile capuchins are skilled foragers from a young age and exploit many of the same foods as adults (MacKinnon, 2006). Capuchins forage in a social context, and while there is much debate about whether capuchins can truly imitate (e.g., Visalberghi and Fragaszy, 1990, 2002; Visalberghi and Limongelli, 1996; Custance et al., 1999; Visalberghi and Addessi, 2003), young animals do intensely observe the behavior of others around them. Therefore, varying group compositions and extended periods of juvenility might allow differing opportunities for observational learning (Whiten, 1989; Custance et al., 1999).

Capuchin physical development is slow compared to other New World monkey species, and the major life history stages occur later when contrasted to similar-sized primates (Fragaszy, 1990; Robinson and Janson, 1987). For example, an adult female *Cebus capucinus* in the wild first gives birth around age seven (Fedigan and Rose, 1995; Fragaszy et al., 2004; Fedigan, pers. comm. and pers. obs). Males at age 7–10 years are still considered subadult but are on the threshold of adult status and are already engaged in sexual mountings with adult females.

Adult capuchins have an unusually large brain for their body size and have well-developed cerebellum, neocortex, and dorsal thalamus areas (Bauchot, 1982;

Passingham, 1973). The sensory and motor cortices that control the hand and the visual cortex are particularly enlarged (Clark, 1960). Such enlargement provides the skills needed for complex manipulative abilities and the construction of object relationships (Gibson, 1990). Thus, capuchins may need a longer period of development for brain growth and cognitive functioning associated with learning their foraging and social behavior repertoires. Among primates, capuchins are especially altricial at birth (Fragaszy et al., 2004). They acquire postural control, prehension and locomotion later than squirrel monkeys, to which they are most closely related, and even later than some Old World monkey species (e.g., baboons and macaques) (Fragaszy, 1990; Bezanson, 2006). Skeletal development is not completed until after the sixth year of life (Jungers and Fleagle, 1980).

As capuchins' immatures develop, certain individuals are preferred for play bouts, foraging partners, grooming partners, and carriers (see Sherrow and MacKinnon, 2011). The juvenile stage is especially important for developing and maintaining early formative relationships: play is common, strong bonds among peers develop, and preferential relationships with certain older animals are formed. As juveniles grow into adolescents, they will begin the transition to either assuming an adult role in the natal group, if female, or transferring out, if male. During this time, they may show an increase in conflict with adult members, rougher and more boisterous play sessions, and an increase in allomothering by females.

Capuchins are a male-transfer species. Even after an individual leaves its birth group, occasional encounters may occur between him and members of his former group. He may leave and return many times or may be followed by a younger juvenile to a neighboring group (Jack, 2003). Parallel dispersal occurs in *C. capucinus* and lasts through multiple migration events (Jack and Fedigan, 2004a, b). Females may occasionally transfer, although it is rare by comparison. Intergroup encounters are common in some areas (e.g., see Jack, 2001 for information on Santa Rosa National Park, Costa Rica), and there is a high likelihood that not all individuals in these groups are strangers to each other. Adult females may have dispersed offspring and siblings in neighboring groups, males may have mothers and siblings, juveniles may have siblings, and adult males have been documented making "visits" to a neighboring group for short periods of time. Male reunion displays have been documented not only among males within a group who are separated for brief amounts of time (captive data for *C. apella*: Phillips and Goodchild, 2005; Matheson et al., 1996; Phillips et al., 1994) but also among males in different groups during intergroup encounters (Jack, 2007; pers. obs.).

Across the *Cebus* species, males and females generally show egalitarian relationships and are characterized as affiliative, with little physical aggression occurring between the sexes. The alpha female usually ranks directly below the alpha male but can dominate over all other males; in several species female coalitions form and can displace the alpha male in context-specific circumstances (Fragaszy et al., 2004). Kinship is an important factor in female–female relationships, although it may not be as important a factor as in cercopithecines. While the overall characteristics of female social relationships are generally consistent across groups and species, male capuchins show extensive variation in their relationships with each other—ranging from despotic to highly cooperative and affiliative. Such diversity reflects

behavioral plasticity in these primates and may be based on shifting ecological (resource abundance/defense) and social (kinship/familiarity) pressures (Janson, 1986).

Mating behavior in *Cebus* is best known in two of the four main species: *C. apella* and *C. capucinus* and is highlighted by elaborately coordinated complex courtship displays that can last for hours (Carosi and Visalberghi, 2002; Jack, 2011). Both conceptive and nonconceptive mating occurs throughout the year, and these behaviors appear to have been co-opted in social exchanges of dominance, affiliation, and perhaps reconciliation (Manson et al., 1997).

As with macaques, interactions based on biological kin, as well as non-kin intra- and intersexual coalition formation and competition are evident components of capuchin social systems (Perry, 1996, 1997, 1998). Because males typically transfer out, social relationships need to be reestablished within their new groups, however many times they switch groups in their lifetimes. Yet, there is evidence that males may also exhibit extended networks of relationships among neighboring groups (see Jack and Fedigan, 2004a, b). Female capuchins who stay in their birth group—and live upwards of 20–30 years in the wild—have a dense constellation of intragroup social networks to keep track of and maintain over the course in their lifetimes. Primates that are highly plastic and variable in their behaviors, and that live in large, multi-male multi-female social groups, have an intricate web of social relationships to remember. Each relationship has its own particular history of positive and negative reinforcements, possible kinship and relatedness factors, and ongoing dynamics. Thus, a form of social niche construction (see Flack et al., 2006) is likely in this genus, given their longevity and complex social landscapes with multiple changing variables.

Capuchins appear to be able to sense fairness in reward/trade situations and value equitable behavior in cooperative situations over rewards in certain tasks (Brosnan and de Waal, 2003, 2004a, b; Brosnan et al., 2006). They are also quite intent on grooming sick/injured individuals of varying rank and are distressed when group members die (MacKinnon, pers. obs.). Thus, they may be astute at empathizing with others' emotional states in varying social contexts—a precondition for altruistic acts. *Cebus* and hominoids share many behavioral and morphological convergences. Given that, do capuchins exhibit any of the core comparison facets (see Table 7.1) for a basal potential for altruism? Recent work on social conventions/traditions in the genus suggests they do. Complex coalitionary behavior exists across the *Cebus* species, with frequent and sustained behavioral exchanges between individuals. For example, males and females generally show egalitarian relationships and are characterized as affiliative, with little physical aggression. Dyadic and triadic interactions occur between and within the sexes; male capuchins in particular show extensive variation in their relationships with each other, ranging from despotic to highly cooperative and affiliative. Extensive visual monitoring and communication (postural, vocal, tactile, visual), grooming, solicited assistance during conflicts, and long bouts of being in contact and/or proximity with others in the group are just some of the daily components of capuchin repertoires. The genus also occupies a broad geographic range, having adaptive success in a diverse array of environments (tropical dry forest, primary rain forest, and living in close proximity to humans).

Table 7.1 Core comparison facets for target primate groups in order to examine basal potential for altruism

Facet	Complex coalitional behavior	Broad geographic range	Behavioral plasticity	Extended period of socially mediated learning
Importance	A basal assumption underlying the potential for altruistic behavior is the occurrence of frequent and sustained behavioral exchanges between individuals	Broad geographic distribution of a primate group across diverse ecotypes/habitats indicates a level of adaptive success representing some ability to ameliorate diverse ecological pressures, possibly niche construction	If we are trying to model the potential emergence of complex and flexible behavior patterns, then one assumes that there must be a strong underlying malleability in the basal neurological and physiological infrastructure for behavioral action	In order to acquire the social skills and apparent “theory of mind” necessary for interpreting others’ complex actions, presumed intentions, and emotional states, a prolonged period of learning in a social context is required

They exhibit a high level of behavioral plasticity. For example, in an examination of cross-site differences in foraging behavior in *C. capucinus*, long-term data from three Costa Rican field sites (geographically close and ecologically similar) identified 30% of shared food items that were processed differently (Panger et al., 2002). Also, in a study that involved a 19,000-hour combined data set (13 social groups, four study sites in Costa Rica, over a 13-year period), several social traditions were identified according to outlined criteria. It is hypothesized that capuchins use these group- or clique-specific social conventions to test the quality of their social relationships (Perry et al., 2003a).

Finally, the genus *Cebus* displays an extended period of socially mediated learning. Evidence suggests that they may need a longer period of development compared to many primate species for brain growth and cognitive functioning associated with learning their foraging and social behavior repertoires. Given the above, it seems plausible that the genus *Cebus* possesses the fundamental and underlying socio-cognitive architecture for basal altruism. . . at least potentially. Living in large complex groups/networks, composed of long-lived, cognitively sophisticated, and behaviorally plastic individuals capable of modifying their social repertoires and histories, positions capuchins well within the range of primate trends discussed here; including the genus *Cebus* in this context provides a Platyrrhine extension to considering social cooperation and (potential) altruism as components of niche construction and social complexity across primates.

Genus Pan

There are two species of chimpanzee: *Pan troglodytes* and *Pan paniscus*, frequently called the bonobo, found across central Africa (Stumpf, 2011). All members of the genus *Pan* are heavily frugivorous (fruit-eating) and their lives are substantially affected by seasonality and fruit abundance. Both species of chimpanzees live in multi-female/multi-male communities ranging in size from 20 to more than 150 individuals. All these individuals are rarely, if ever, in the same location at the same time, however. Chimpanzee communities are characterized by a *fission–fusion* social pattern, meaning that individuals spend their time in various subgroups, which have variable compositions across space and time. Both species are characterized by female dispersal and male philopatry, although there is some female philopatry in at least a few eastern chimpanzee populations (Stumpf, 2011).

Subgroups generally consist of mixtures of age and sex classes. Mother–offspring subgroups are made up of an adult female and her dependent offspring (usually a youngster under 7 years of age). Multi-female subgroups consist of multiple adult females and their offspring. Subgroups made up of clusters of related individuals consist of females and their offspring, some of whom may be adult or at least independent of the mother. All-male subgroups are made up of multiple adult and sometimes subadult (teenage) males. Heterosexual subgroups consist of adult males and females and frequently young individuals. Consort pairs are two adult individuals (usually one male and one female) who separate themselves from other individuals in the community and spend a good deal of time mating. Finally, individual chimpanzees occasionally move around the range of their community by themselves.

In *P. troglodytes*, males are, on average, dominant over females; however, both males and females compete with others of their sex and establish hierarchical ranks (Stumpf, 2011). Males attain high rank by forming alliances and coalitions with other males (frequently those of similar ages) and by using spectacular displays and other intimidation tactics, including serious fighting, to manipulate other members of their community into ceding access to favored resources. Male competition for rank can result in serious injuries and occasionally death. Some males attain rank through extreme aggression and maintain that behavior once they are high ranking. Others appear to rely heavily on coalition partners and mutual grooming and social bonding to achieve and maintain dominance status. For females, dominance is associated with substantially improved access to food sources and high infant survivorship (especially in east African populations). High-ranking females tend to have a large number of offspring in the group, and occasionally mother–daughter pairs act together to achieve or maintain high rank. Females do achieve dominance via aggressive displays and occasionally fighting, but they do not do so as frequently or intensely as males. In east African *P. troglodytes*, both males and females who are high ranking gain access to favored food sources and social partners and therefore have increased reproductive success. In West African forms, rank does not always result in increased reproductive success (Boesch et al., 2002; Stumpf, 2011).

In *P. paniscus*, dominance contests, dominance relationships, and the overall tenor of rank are different than in *P. troglodytes*. In this species, females are generally dominant to males and put on substantial dominance displays in which they drag tree branches or other objects behind them (White, 1996; Furuichi, 1997). However, dominance interactions rarely result in serious fighting. Rather, many of the dominance interactions and other conflicts in this species are resolved via genital–genital rubbing and other sociosexual behavior (Kano, 1992; Parish, 1996). Male bonobos also have an intrasexual dominance hierarchy, but they are seldom dominant over females. A male's rank is frequently tied to that of his mother. Males do compete with one another aggressively at times, but compared with *P. troglodytes*, bonobos show lower overall rates of aggression (Furuichi and Ihobe, 1994).

Although females disperse in both species, strong bonds between unrelated females are common in *P. paniscus* and fairly rare in *P. troglodytes* (Parish, 1996; Stanford, 1998; Kano, 1992). This difference may have to do with the differences in dominance systems and in the way that community members treat recent migrants in the two species.

Both species of the genus *Pan* hunt and eat other mammals, but *P. troglodytes* does so more frequently than *P. paniscus*. Hunting appears to coincide with times of fruit abundance, suggesting that meat may not be merely a nutritional supplement. Although females hunt in both species, it is an activity performed predominantly by males in *P. troglodytes*. Populations of *P. troglodytes* in western Africa hunt in a more coordinated manner than those in eastern Africa (Boesch et al., 2006; Stanford, 1998). Hunting success rates seem to be related to the size of the subgroup doing the hunting, with larger parties being more successful. When kills are made, the meat is frequently shared among a few individuals, usually the coalition partners and allies of the successful hunter. Occasionally, if the kill is made by a low-ranking individual, then a high-ranking male may steal the kill and not share any with the actual hunter. Interestingly, infanticide (killing of infants) and cannibalism are both reported for *P. troglodytes*. There are cases in which adult females and males have captured, killed, and eaten infants from their own community and from females of neighboring communities. When an infant is killed and consumed, it is treated very much like a colobus monkey that has been hunted and captured.

In populations of *P. troglodytes* in eastern Africa, researchers have reported incidents of intercommunity conflict that resulted in deaths. “Border patrols,” or groups of males moving along the communities' geographic boundaries, are reported for most, but not all, populations of chimpanzees. It has been hypothesized that these “patrols” are subgroups of males searching for small subgroups or lone individuals from neighboring communities. Occasionally, when these subgroups encounter individuals from another community, they attack as a mob. It is hypothesized that these attacks are an effort to increase the community's access to desired resources and that chimpanzees strategically assess the relative “power” of their neighbors in attempts to increase their ranges (Stumpf, 2011; Wilson and Wrangham, 2003).

Genus Homo

Homo sapiens are found distributed across nearly all habitable areas on the planet. The species exhibits a startling high degree of morphological variation while simultaneously demonstrating relatively little inter-population genetic variation (Fuentes, 2006; Long et al., 2009, Relethford, 2009). Humans live in mixed sex groups ranging from less than 50 individuals to many thousands of individuals in areas where they have undertaken substantial ecological engineering (villages, urban zones etc.). Human behavioral, dietary, and social plasticity exceeds all other living animals. Patterns of intergroup transfer, mating, alliances and coalitions within and between groups, social hierarchies, politico-economic systems and all manner of social structures vary in human societies across the globe. Humans are amongst the slowest developing primates, with extensive social learning core to a complex ontogenetic sequence involving linguistic and symbolic as well and more general behavioral instruction. Tool use and manufacture along with extensive extra-somatic manipulation of the environment is standard for all human groups with massive niche alteration and construction ongoing throughout our evolutionary history and more recently and regularly at an accelerated pace across local, regional, and global levels.

Primate Trends and Human Patterns: Overlap, Differences, and Evolutionary Implications

The above taxonomic examples highlight important facets of social complexity and map to our notions of social niche construction and social networks. Specifically, complex coalitionary behavior, inhabiting a broad geographical range, high levels of behavioral plasticity, and an extended period of socially mediated learning are all malleable and can change rapidly from one generation to the next (or stay in stasis). Being able to accommodate such potential change underscores the adaptive advantage of social networks in terms of functioning as a niche construction *mechanism* (see Fuentes et al., 2010).

Humans are primates, yet we display a wide array of significant differences, especially at the level of social complexity and relative frequency of altruistic behavior (or at least apparently altruistic behavior). How can we envision the derivation of the modern human system in line with the phylogenetic connections to other primates?

The earliest human ancestors existed in multi-adult groups with a relatively high degree of social complexity, patterns of social bonding between individuals within the group, and a level of inter-individual cooperation and competition at least equal to that found in ape and monkey societies. Individuals exhibited substantial behavioral flexibility, at least as much as the modern apes, and a repertoire of vocal and gestural communication, but not language. Rudimentary tool use and manipulation of the environment was present as was sexual dimorphism in size, with males being larger than females resulting in some differences in behavioral roles between

males and females. However, specific patterns of dominance relationships between individuals are not clear. These earliest human ancestors shared with their primate cousins specific type of “social intelligence” (Dunbar and Shultz, 2007). Humans stand apart via the *vast amount* of information that is disseminated socially through space *and* time (via spoken/written language characterized by abstraction and symbolism). In the relatively brief period of evolution for the genus *Homo*, we have been able to dramatically alter/manipulate myriad environments (affecting our survival on a populational level via predator avoidance, better food acquisition, cultural complexity, increased infant survivorship, and overall group health) in a short amount of time (Fuentes et al., 2010). We are also characterized by the most extended period of infant dependency and development in our order, including a protracted period of brain maturation. It has been suggested that an extension of the primate social intelligence hypothesis to reflect the fact that humans are “ultra-social” would be useful, resulting in what some have called the cultural intelligence hypothesis (Herrmann et al., 2007). So, where all primates have evolved social-cognitive skills for cooperating and competing with group/community members, humans have also evolved skills for establishing distinct cultural groups, with different physical and symbolic markers (social institutions, artifacts, language, etc). While primates transmit many behaviors socially (see Whiten et al., 1999; Panger et al., 2002; Perry et al., 2003a, b; Preutz and Bertolani, 2007, and van Schaik et al., 2003), their species-typical cognition does not require participation in specific cultural interactions in the same way as it does in humans (Tomasello, 1999). Only humans have a *species-specific* set of social-cognitive skills (that emerges early in ontogeny) for participating and exchanging knowledge in cultural groups (see Herrmann et al., 2007). [However, as Boesch (2007) points out, most claims of human cognitive uniqueness are based on comparisons of White middle class Westerner humans (*H. sapiens*) with captive chimpanzees (*P. troglodytes*).] Thus, the extent to which our biological and cultural traits are intertwined and embedded in our species’ evolutionary history is unique among primate taxa.

In summary, the potential for altruism—or even just the basal proclivity toward an altruistic ability—is likely present in many primate lineages and potentially reflects a gradient of the “cultural mind as niche construction” concept. We have attempted to highlight here the plasticity and resulting adaptability in each of the four genera and propose that bonding and cooperation play a significant role in social niche construction among primates.

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