

EVOLUTION AND CONSEQUENCES OF SOCIALITY

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Many animals live in social groups rather than solitarily, mainly because group living decreases the risk of predation. Minimizing predation risk—rather than, for instance, maximizing resource intake—is particularly important for species with slow life histories, who grow up slowly, reproduce late, and live for a long time. Individuals from such a species may succumb to predation before they have successfully reproduced, which obviously bears fundamental fitness costs. It is thus not surprising that primates, with their slow life histories, have a strong priority to minimize predation risk and are particularly social, having evolved diverse and sophisticated social systems. A hallmark of primate societies is that they are not merely loose aggregations of individuals but are instead stable arrangements that contain individuals who develop social bonds; this social complexity has been argued to be linked to, or even drive, cognitive complexity.

In this chapter, I first overview the factors that drive the evolution of social systems, particularly in primates. I then turn to the consequences of sociality, reviewing the empirical data that support a link between social complexity and cognitive evolution. Traditionally, such links have followed a benefit perspective, in which it is argued that investing in brain tissue and thus cognitive power is driven by direct benefits in the social realm, such as being able to outwit group members and thus to cope with the less advantageous aspects of group living. It is becoming increasingly clear, however, that variation not only in benefits but also in costs has to be considered to understand the evolution of big brains.

Brains are special, not only because they are incredibly costly organs but also because there is no direct link between the size of a given brain and the amount of fitness-relevant skills it actually produces for an individual. Although bigger brains potentially produce more and more diverse skills, it is important to keep in mind that many such skills have to be acquired ontogenetically, via learning. The more efficiently this learning takes place, the higher the fitness benefit of having a bigger brain will be. According to the broad version of the cultural intelligence hypothesis (van Schaik & Burkart, 2011; Whiten & van Schaik, 2007; see also Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007, for the version that focuses on humans and other great apes), sociality plays an important role for this translation of brain tissue into fitness-relevant skills because social learning is much more efficient for the acquisition of survival-relevant skills when compared with individual learning. The broad version of the cultural intelligence perspective thus complements the traditional benefit hypotheses for the evolution of intelligence because it specifies the conditions under which potential benefits are more likely to outweigh the costs of evolving a bigger brain, namely when social learning canalizes the ontogenetic translation of brain tissue into survival-relevant skills.

Extensive allomaternal care, or cooperative breeding, refers to social systems in which individuals other than the mother help rearing offspring, which can alleviate the energetic and life history costs (see Chapter 3, this volume). Furthermore, the social

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dynamics in cooperatively breeding primate groups are particularly conducive to social transmission of skills because they are characterized by high levels of social tolerance, tendencies toward proactive prosociality, and attentiveness between all group members (see below). Thus, although engaging in cooperative breeding per se does not require more complex cognitive skills than independent breeding, the facilitation of social transmission of skills in such societies is likely to remove constraints that prevent the evolution of bigger brains in independently breeding species.

An integrated perspective on the consequences of sociality on cognitive evolution thus not only focuses on direct benefits but also takes into account costs and constraints. Large data sets that quantify potential costs, benefits, and constraints for a large number of species make it increasingly possible to disentangle the impact of these different factors and thus to more precisely elaborate the links between sociality and brain evolution (see Chapters 12 and 24, this volume).

In the last section, I turn to humans, a primate characterized by both high social and cognitive complexity. My aim in this last section is to use this integrated perspective based on comparative data to evaluate to what extent human social and cognitive

characteristics can be understood as resulting from primate-general regularities.

ORIGINS AND DETERMINANTS OF SOCIALITY

Almost all animals share the same basic set of ecological and social challenges: finding food and avoiding predators, avoiding disease and maintaining thermoregulation, and finding a mate and rearing viable offspring. How these challenges are met can be influenced by how animals interact with others: Social life is above all affected by whether the individual is solitary or lives in a group. The most important and influential consequences of group living are, on the one hand, reducing the risk of falling victim to predation and possibly improving thermoregulation but, on the other hand, increasing feeding competition (van Schaik, 1983). Additional costs and benefits of group living (see Table 13.1), however, also contribute to determining to what extent animals are gregarious, as well as the specific form that these groupings take.

More important, these costs and benefits do not apply equally to all species, or all individuals in any given species, but are influenced by additional factors, such as the kind of social grouping and sex,

TABLE 13.1

Benefits and Costs of Group Living With Regard to Various Ecological and Social Challenges

Challenge	Consequences of group living	
	Benefits	Costs
Avoiding predators	Shared vigilance, faster detection of predators Dilution of risk, confusion effect, safety in numbers Collective defense, mobbing	Higher conspicuousness
Finding food	More efficient detection of food sources Cooperative and communal exploitation and defense	Competition over access to food
Avoiding disease	Reduced ectoparasite loads (grooming)	Easy transmission of disease and parasites
Thermoregulation	Reduced heat loss	
Finding a mate	Easy access	How to avoid inbreeding? → dispersal strategies Competition over mates
Rearing young	All ecological benefits Socialization: availability of play partners Access to helpers Access of young to information	All ecological costs

Note. Data from Lee (1994) and van Schaik (2016).

size, experience, and dominance of the individual, which modulate how the different ecological and social challenges are weighted (see Chapter 7, this volume). The balance between the fitness costs and benefits across all these domains will ultimately determine a species' way of life (Lee, 1994; Mitani, Call, Kappeler, Palombit, & Silk, 2012).

Animal groupings vary significantly. Some simply consist of temporary, anonymous aggregations such as flocks or herds; others are anonymous but more stable over time, as for instance in fish schools; yet others are both stable and personalized, as is typical for primates, carnivores, or equids. The kind of grouping in a given species obviously modulates the costs and benefits associated with it. For instance, safety-in-numbers effects are present in any large aggregation, whereas cooperative hunting and prey defense is a benefit that is usually only achieved in stable and personalized groups.

Sex differences in the importance of the different ecological and social challenges represent an important additional layer of complexity for understanding the evolution of sociality. According to Bateman's (1948) principle, a male's reproductive success is fundamentally limited by access to mates, whereas females' reproductive success is limited by access to food and safety. Females therefore are expected to use social strategies that improve access to food and safety, whereas males should use strategies to improve access to females. According to the socioecological paradigm, the females, as the "ecological" sex, thus choose strategies linked to environmental conditions, whereas the optimal male strategy depends on the females' distribution and behavior (Schuelke & Ostner, 2012).

In general, safety, especially that of dependent offspring, is best achieved in large groups, whereas foraging is more efficient when performed alone. This is because in each group, food competition has both a contest (dominance) and a scramble (pure group size effect, with dominance effect removed) component. Thus, in larger groups, all suffer more feeding competition than in smaller groups, although the burden usually falls more heavily on the subordinates. Females will thus adjust their behavior to find the optimal balance between the two. Where exactly this equilibrium is situated for

a given species depends on additional factors. For instance, body size and life history have an impact on susceptibility to, and acceptable risk of, predation. Similarly, when food is clumped and highly valuable, contest competition typically increases, which in stable and personalized societies tends to lead to the formation of dominance hierarchies. In societies with steep dominance hierarchies, valuable alliances, close bonds, and female philopatry typically coevolve (van Schaik, 1996).

Finally, all these factors cannot be considered in isolation but need to be considered in their historical context. Evolutionary options are not equal for all species, but ancestral states heavily constrain the degrees of freedom for evolutionary trajectories. Primate social behavior, for instance, shows strong evidence for phylogenetic inertia (Shultz, Opie, & Atkinson, 2011). As a consequence, predicting the form of societies on the basis of the costs and benefits of associating with others is far from straightforward. Nevertheless, the socioecological approach has been and still is a useful framework for investigating and understanding the evolution of sociality, and this approach has been particularly fruitful in primatology.

DIVERSITY OF PRIMATE SOCIAL SYSTEMS

Compared with other mammals, primates are a particularly social taxon. Taxonomists currently recognize 16 families, composed of 77 genera and 488 species, spread over Africa, South America, Asia, and Madagascar (Rylands & Mittermeier, 2014). Primates display spectacular social diversity and complexity. In fact, all diurnal primates live in some form of stable social grouping, ranging from semisolitary orangutans to small pair and family units; larger groups structured around hierarchically organized matrilineal units; and huge multilevel societies composed of hundreds of individuals (Mitani et al., 2012). An impressive amount of work has been put into understanding how this diversity is linked to ecological challenges, such as finding food and avoiding predators, and how they interacted in shaping the evolution of primate sociality, life history, and development (Mitani et al., 2012; Schuelke & Ostner, 2012; Swedell, 2012; van Schaik, 1996, 2016; see also Chapter 7, this volume).

The origin of this extraordinary sociality can best be understood as a consequence of the slow life history of primates: Primates grow up more slowly, reproduce later, have smaller litters, and live longer lives than mammals of similar body size (Isler & van Schaik, 2012a). Species with a slow life history must have a strong priority for minimizing predation risk—rather than, for instance, maximizing resource intake—because their fitness is highly dependent on a long life span.

The necessity of minimizing predation risk in species with a slow life history follows from the fact that different life history traits such as growth rates, age at first reproduction, or life span cannot evolve independently but come as a syndrome, where all traits are tightly linked to each other (Stearns, 2000; van Schaik & Isler, 2012). The critical determinant of the pace of life history is the level of unavoidable extrinsic mortality (e.g., through predation, starvation, or disease). Arboreal species, compared with terrestrial animals of the same size, are less subject to unavoidable extrinsic mortality, because they are confronted with fewer predators and have more escape routes and hideouts and generally face lower disease exposure (van Schaik & Isler, 2012). Primates originated as an arboreal lineage, and most contemporary primate species still are.

In species with high unavoidable extrinsic mortality, it does not pay to invest heavily in physiological mechanisms that allow a long life span and thus a slow life history. In these species, the evolution of slower life history is prevented, whereas in species with lower extrinsic mortality, such as arboreal species, an evolutionary process leading to reduced extrinsic mortality can ensue. Sociality functions to further reduce extrinsic mortality risk and may therefore lead to even slower life histories. The high sociality of primates can thus be best understood as a consequence of this arboreality, which enabled the evolution toward slow life histories. With a slow life history in place, prioritizing the minimization of predation risk becomes a necessity, and group living is the solution of choice to achieve this. The coevolutionary process between extrinsic mortality and mortality-reducing measures (with their costs) will reach a different equilibrium in each species (van Schaik & Isler, 2012).

Primates typically do not live in loose aggregations but in stable and bonded groups, where individuals recognize each other. Moreover, unusual among mammals, primates tend to live in groups containing both sexes, adding potential social complexity (van Schaik & Kappeler, 1997). Their social behavior in the group is often based on sophisticated social cognition (see Chapters 42 and 44, this volume), and their slow life history allows for the establishment of long-term relationships and bonds, which can have measurable fitness consequences for individuals (Silk, 2007) and have been argued to facilitate the evolution of cooperative behaviors, including coalition formation, and of large brains.

In fact, the consequences of sociality for the evolution of cognition and large brains have received enormous amounts of research effort, not least because humans stand out among the other primates with respect to both. A better understanding of these evolutionary relationships therefore also has the potential to elucidate the evolutionary trajectories that led to the uniquely human sociality and cognition. In the next section, I therefore overview the various conceptualizations of such a link between sociality—or social complexity—and cognition, as well as the comparative empirical evidence supporting them. Finally, in the last section, I explore the explanatory power of this body of work for the specific case of humans.

CONSEQUENCES OF SOCIALITY: FROM SOCIAL TO CULTURAL INTELLIGENCE

The intense sociality of primates is striking, often visible in complex social behaviors that are based on sophisticated social cognition (see Chapters 42 and 44, this volume). It is thus not surprising that from early on, researchers have hypothesized that challenges from coping with the social world, rather than ecological challenges, were responsible for the evolution of primate intelligence and thus brain size. The social intelligence hypothesis has a long history (Chance & Mead, 1953; Humphrey, 1976; Jolly, 1966) and comparative empirical evidence has indeed shown an association between various measures of social complexity and brain size (Byrne & Whiten, 1988; Dunbar, 1998; Dunbar &

Shultz, 2007a), which has led to near universal acceptance of this hypothesis for primates and other mammals.

Social Benefits as a Driver for Cognitive Evolution

Different versions of the social intelligence hypothesis stress different social benefits. The Machiavellian intelligence hypothesis, for instance, argues that cognition evolved to better cope with the costs of group living, such as increased competition for food or mates (Byrne & Whiten, 1988). Individuals who are better able to manipulate or outwit others for their own benefit, and are able to do so without destroying their group or being expelled, will have a fitness advantage. In stable and bonded groups with individual recognition, this is particularly demanding and can be achieved by deception (Byrne & Corp, 2004), but also by alliance formation and more subtle social strategies that may involve strategic sharing of food or grooming. The social brain hypothesis (Dunbar, 1998; Dunbar & Shultz, 2007a, 2007b) more generally emphasizes the computational demands of living in large, complex societies that are based on bonded relationships between group members (e.g., memory for a large number of individually recognized faces, or processing information about a set of individualized relationships). The cultural intelligence perspective finally focuses on the impact of social learning and transmission. The cultural intelligence hypothesis has been developed for cognitive development and evolution in humans, where it is supported by species-specific sociocognitive adaptations (Herrmann et al., 2007), but also as a more general principle for primates (Whiten & van Schaik, 2007) and other animals, such as birds (van Schaik, Isler, & Burkart, 2012).

Despite the broad support and acceptance of the social intelligence hypothesis, it still faces several challenges (van Schaik et al., 2012; see also Chapter 12, this volume). First, a considerable amount of variation in brain size remains unexplained in comparative analyses. Orangutans, for instance, who are among the largest brained primates, are at the same time among the most solitary primate species. Not only single cases such as the orangutan remain unexplained, however; the hypothesis also cannot

account for so-called grade shifts (i.e., differences at higher taxonomic levels). For instance, why do diurnal lemurs have smaller brains than monkeys? Diurnal lemurs live in large groups based on individualized relationships, including dominance hierarchies comparable to those in monkeys. Likewise, it remains unexplained why apes have bigger brains and are smarter than monkeys (Reader, Hager, & Laland, 2011) because apes live in smaller groups than many monkeys and are not systematically more likely to engage in coalitions.

Second, bigger brains in primates are associated not only with better sociocognitive abilities but also better performance in both social and nonsocial contexts, including tool use and innovation (Reader et al., 2011), which is not expected if benefits from the social domains alone are decisive in whether a species evolves a bigger brain. In fact, there is some evidence suggesting that, in principle, sociocognitive solutions to problems in the social domain can evolve separately and without requiring particularly large brains (e.g., bats [Baigger et al., 2013], fish [Bshary & Brown, 2014], hyenas [Holekamp, 2007]).

One way to address these challenges is to explore whether, in addition to benefits in the social domain, ecological benefits also played a role, thus integrating a contribution of ecological challenges in models of cognitive evolution (Holekamp, 2007; Reader et al., 2011; Shultz & Dunbar, 2006; see also the cultural intelligence hypothesis as detailed below). These ecological challenges may have co-occurred with social ones or acted in sequence. For instance, Byrne (1997) proposed that, after selection for enhanced social intelligence in apes, more recent ecological challenges in the food processing context may have selected for enhanced technical skills. However, including additional potential benefits in the models is not enough for a comprehensive understanding of brain evolution and the role of sociality therein. Such a comprehensive understanding requires a focus not only on the benefits of having bigger brains and more cognitive power but also on the costs and constraints that may prevent the evolution of bigger brains despite tractable potential benefits (Charvet & Finlay, 2012; Isler & van Schaik, 2014).

A Broader Framework That Also Takes Costs Into Account

Bigger brains not only come with benefits to better cope with social and ecological challenges but also have considerable costs, which include energetic, life history, and demographic aspects (Isler & van Schaik, 2014). First, brains consume a large proportion of the energy available to an organism, in particular during ontogeny (Kuzawa et al., 2014). This energy has to be provided constantly, because brains cannot be starved for some period of time when no food is available; brain starvation causes permanent damage, again in particular during ontogeny (Lukas & Campbell, 2000). The energetic costs are thus particularly high in immatures.

Second, by competing for energy with other allocation targets, bigger brains might slow down development and reproduction and thus the pace of life history. Indeed, brain size is empirically associated with slower development, a later age at first reproduction, and reduced reproductive rates, which have to be compensated for by a longer adult life span. Crucially, this implies that only species able to slow down its life history will be able to respond to a selective pressure for brain enlargement, such as a potential social or ecological benefit. This effect is also known as the life history filter (van Schaik et al., 2012): Several lineages who face identical cognitive challenges may nevertheless not all evolve the same cognitive adaptations and brain enlargement because they differ regarding whether they are able to adopt a slower life history. The possibility of slowing down life history is thus a fundamental constraint on brain evolution, and whether a species is able to do so critically depends on the risk of unavoidable extrinsic mortality due to unpredictable exposure to disease and unavoidable predation.

Finally, lineages that are able to slow down their life history and evolve large brains may face demographic costs. Because of their slow life history, their populations can only grow very slowly, and they have a low maximum rate of population increase. This is particularly problematic when population size suddenly declines, in the case of population crashes, because the population is less likely to recover. Moreover, populations cannot quickly adapt to changing environmental conditions and are

thus more likely to exceed the limits of their phenotypic plasticity and go extinct (van Schaik, 2013). There is thus a limit to the evolution of ever bigger brains, a gray ceiling above which populations are no longer viable. Intriguingly, our hominin ancestors were able to break through this gray ceiling. I will come back to this below and discuss how a specific form of sociality, cooperative breeding, played a crucial role in doing so.

Brains are thus very expensive organs with regard to energetic demands as well as life history and demographic costs. Given these considerable costs, species who need less brain tissue to add a cognitive skill will have an advantage and will be better able to respond to social and ecological cognitive challenges. Variation in this is possible because brains possess yet another peculiarity: What is heritable, and malleable by natural selection, is the brain and its potential to invent effective solutions to problems. However, what contributes to fitness is not the ability to learn or innovate per se but rather the acquisition and production of innovative solutions: the learned skills that must be acquired ontogenetically de novo by every individual. Rare, serendipitous inventions by a single individual may make major contributions to the fitness of this individual, but they are not heritable. What makes such innovations heritable is social learning. According to the cultural intelligence hypothesis (Herrmann et al., 2007; Tomasello, 1999), humans have evolved specific adaptations to the acquisition of cultural knowledge, which played an important role in human cognitive development and evolution. However, this process can be generalized, and in its broad version, the hypothesis posits that species who engage in social learning are more likely to respond to cognitive selective pressures (van Schaik & Burkart, 2011; van Schaik et al., 2012; Whiten & van Schaik, 2007).

The rationale behind this broad version is that compared with individual learning, social learning more reliably translates additional, highly expensive brain tissue into survival-relevant skills: If additional brain tissue is invested in individual learning, it is still likely that bigger brained individuals fail to invent survival-relevant skills despite their higher cognitive potential. The reason for this is that the

invention of a successful skill or innovation depends not only on cognitive ability (and thus brain size) but also on the exposure to relevant stimuli, as well as on stochastic events in the environment. In contrast to individual learning, social learning makes survival-relevant skills themselves heritable. Thus, if additional brain tissue is used to increase social learning, the translation of additional brain tissue into survival-relevant skills becomes much more reliable and efficient, and the same amount of brain tissue will result in a larger set of survival-relevant skills (see Figure 13.1). The strength of this effect depends on the forms of social learning (see Volume 2, Chapters 19 and 20, this handbook) available to a species, but in principle any form of social learning is effective.

The broad version of the cultural intelligence hypothesis is supported by empirical evidence (Reader et al., 2011; van Schaik & Burkart, 2011) showing that, ontogenetically, the number of learned skills acquired by maturing individuals indeed depends on its opportunities for social learning. Phylogenetically, it predicts that selection will most likely favor the evolution of improved domain-general cognitive abilities in lineages with social learning and should do so to a greater extent with more prevalent opportunities for social learning.

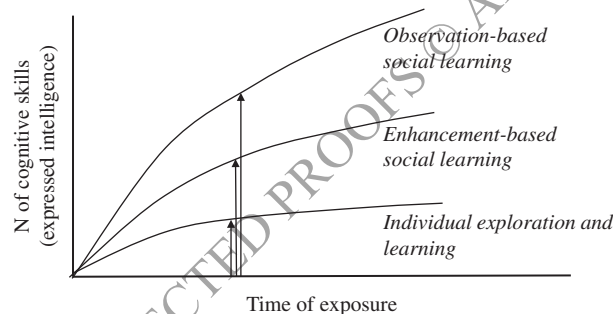


FIGURE 13.1. Developmental conditions and cognitive performance when using individual versus social learning. The longer an individual is exposed to a specific problem space, the more likely it is to develop a solution to this problem (expressed intelligence) based on individual exploration and learning. However, if it can observe other individuals solving this problem, much shorter exposure time is needed, in particular if observational forms of social learning such as imitation are used. Note, however, that any form of social learning will optimize skill acquisition relative to individual learning.

Empirical evidence has supported these phylogenetic predictions, too. The cultural intelligence perspective can thus explain why big primate brains that perform well in social contexts also perform well in nonsocial contexts, which is more difficult with an exclusive focus on benefits only.

In this broader framework, it thus becomes evident that whether a lineage responds to a social or ecological challenge by evolving a bigger brain depends not only on the potential benefits but also on how well this lineage can accommodate the associated energetic, life history, and demographic costs and to what extent it engages in social learning. Keeping this in mind, I now turn to a specific form of sociality, cooperative breeding. Cooperative breeding is a particularly important form of sociality in the present context because it can alleviate some of the above-mentioned constraints that prevent the evolution of larger brains.

A Particularly Relevant Form of Sociality: Cooperative Breeding and Its Consequences

In mammals, including primates, the prevalent pattern of rearing offspring is that the mother alone cares for the offspring until it becomes independent. In some species, however, other individuals help to care for and provision the offspring (Solomon & French, 1997; see also Chapter 3, this volume). Allomaternal care varies across species, from small contributions by a few individuals to systems in which the majority of infant care is provided by nonmothers. Cooperative breeding systems are located at one end of this spectrum. Broadly defined, they refer to reproductive systems in which group members other than the parents contribute to rearing offspring (Hrady, 2009). Extensive allomaternal care can affect the cost–benefit balance of big brains by alleviating energetic, life history, and demographic costs and by facilitating social learning.

Extensive allomaternal care can alleviate the costs of big brains. An evolutionary increase in brain size within a lineage is only possible when extra energy can be made available (Isler & van Schaik, 2009, 2014). The energetic costs of brains are particularly high for developing immatures, who have to

allocate a larger proportion of their energetic intake to the brain compared with adults. In independently breeding species, the energy available to immatures is limited by what the mother is able to provide. In cooperative breeders, this limitation is offset because the maternal contributions are supplemented by the energy subsidies from alloparents who provision food. This energetic benefit may in principle also accrue when provisioning is exclusively performed by the genetic father, as long as the contributions are substantial. The relevant feature here, therefore, is extensive allomaternal care rather than cooperative breeding defined according to some more narrow definitions, such as extreme reproductive skew due to suppressed reproduction in the helpers (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2009).

Extensive allomaternal care also has life history consequences. The load reduction of mothers supplied by helpers allows females higher reproductive rates. In nonhuman primates, higher levels of allomaternal care are correlated with shorter gestation and lactation periods and higher reproductive rates (Isler & van Schaik, 2012a; Mitani & Watts, 1997; Ross & MacLarnon, 2000). This pattern is particularly striking in the cooperatively breeding callitrichid monkeys, who exhibit the highest level of allomaternal care among nonhuman primates and the highest reproductive rates. After a short gestation time (relative to body size) of less than 5 months, callitrichid monkeys usually give birth to twins (rather than singletons, which is the case in all other primates). Furthermore, females show no lactational amenorrhea but experience a postpartum estrus and can thus get pregnant again almost immediately after giving birth (Digby, Ferrari, & Saltzman, 2007). Mothers can afford these high reproductive rates only because other group members help by carrying the infants and sharing food. Nevertheless, the reproductive burden of mothers is high because the surplus energy provided by alloparents is directly invested into a higher number of offspring. Despite this fast-paced reproduction, immatures show relatively long periods of dietary dependence, for instance, compared with the more independently breeding squirrel monkeys or the owl and titi monkeys among whom nonparental individuals usually do not contribute to infant rearing

(Garber, 1997; Garber & Leigh, 1997). Cooperative breeding thus enables a peculiar mix of life history traits. In particular, fast reproductive rates can coexist without a shortening of the developmental periods because others step in with energy subsidies when mothers are already engaged with the pregnancy of the next set of offspring.

In sum, extensive allomaternal care has several energetic and life history consequences relevant for the evolution of larger brains. First, energy subsidies by allomothers help immatures pay for the energetic costs. Second, the load reduction of mothers through allomaternal care can be used in two ways, each of which is supported by broad phylogenetic comparisons: to invest in higher reproductive rates, as are found in birds and mammals and particularly in nonhuman primates, or to invest in brainier offspring, as is found in mammals in general (particularly so in carnivores, but not in nonhuman primates; Isler & van Schaik, 2012a).

Motivational and cognitive consequences of cooperative breeding. At a more proximate level, cooperative breeding can also improve social learning. This is possible if behavioral tasks related to cooperative breeding require adaptations at the psychological and motivational levels, such as higher social tolerance and proactive prosociality (see Chapter 44, this volume), which in turn facilitate social transmission (Burkart & van Schaik, 2010; Snowdon, 2001).

High social tolerance is necessary in cooperatively breeding primates among whom alloparents contribute by carrying infants and sharing food. The necessary spatial and temporal behavioral coordination in the transfer of infants from one caregiver to the next leaves no room for tension between the caregivers because unsuccessful transfers have potentially lethal consequences for the infants. Because most of the time all animals in the group contribute to infant carrying, high social tolerance is necessary between all dyads in the group. Another task linked to cooperative breeding in primates is food sharing. Food sharing in callitrichids is substantial, in particular compared with independently breeding primates (Brown, Almond, & van Bergen, 2004; Jaeggi, Burkart, & van Schaik, 2010). The

first solid food that infants ingest is food shared by a caregiver, and weekly experimental food-sharing trials have shown that during the main provisioning period, adults share 53% of all items they obtain with the immatures (breeders = 61%, helpers = 46%; Martins & Burkart, 2013). In food-sharing interactions, adults allow the offspring to take some of their food, which again requires a high level of social tolerance. In addition, and in contrast to independently breeding primates, adults also proactively offer food to immatures by holding the food in their outstretched hand, emitting a specific food call, and waiting for the immature to come and take it. Proactive food offering cannot be explained by high social tolerance alone because social tolerance is a fundamentally passive attitude and thus not able to actively motivate actions. Proactive food offering thus seems to require an additional, prosocial motivational element, such as proactive prosociality.

Is such a link among social tolerance, proactive prosociality, and allomaternal care supported by empirical data? The existence of particularly high levels of social tolerance in cooperatively breeding primates has been pointed out repeatedly (e.g., Garber, 1997; Schaffner & Caine, 2000; Snowdon 2001), and some, albeit not all, results from prosociality studies have pointed in the same direction (Cronin, 2012). Because directly comparable data were available for only a few species and diverse methodologies often prevented direct species comparisons, Burkart and Rueth (2013) collected social tolerance and prosociality data for 24 groups of

15 primate species in exactly the same way and used phylogenetically controlled analyses to assess whether they were linked to the extent of allomaternal care. Figure 13.2 shows that the extent of allomaternal care indeed predicts social tolerance and proactive prosociality. For social tolerance, it is a better predictor than any of the other factors that have been proposed, including high cognitive ability and thus brain size, the presence of strong selective social bonds, a fission–fusion social system, or the need to coordinate behavior in the context of foraging (Burkart et al., 2014). Figure 13.2 also shows how allomaternal care increases social tolerance, although there may also be other sources of high social tolerance, as shown by the high values of the pair-bonded gibbons (*Hyllobates*).

Callitrichid monkeys not only cooperate in carrying infants and sharing food but also share vigilance duties (Goldizen, 1987; Koenig, 1994), engage in cooperative food harvesting, and show more cooperative territory and resource defense than independently breeding primates (Garber, 1997; Willems, Hellriegel, & van Schaik, 2013; Willems & van Schaik, 2015). To coordinate the various cooperative activities within the group, it is necessary to systematically pay attention to the location and behavior of the group members (i.e., to engage in frequent social monitoring; Snowdon, 2001). Social monitoring is important for more despotic primate species, too, to continuously monitor dominant individuals, particularly in situations of potential conflict. In cooperatively breeding primates,

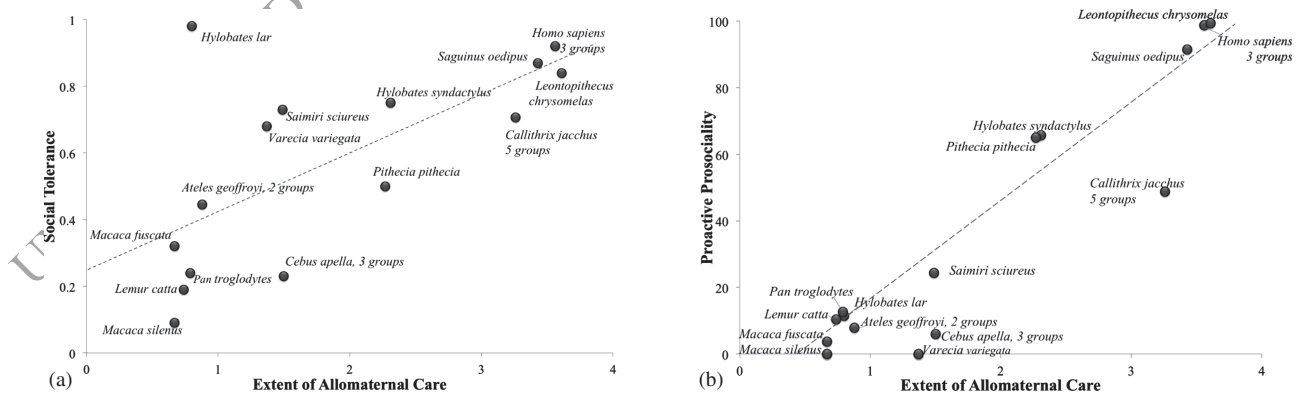


FIGURE 13.2. In primates, social tolerance (a) and proactive prosociality (b) are correlated with the extent of allomaternal care.

however, social monitoring need not be directed at dominant individuals and, more important, it also occurs at high rates in relaxed social contexts.

Together, high social tolerance, proactive prosociality, and an attentional bias toward the behaviors and whereabouts of group members in a relaxed way can facilitate social learning. The facilitating effect of social tolerance on social learning has long been emphasized (Coussi-Korbel & Fragaszy, 1995; Schwab, Bugnyar, Schloegl, & Kotrschal, 2008; van Schaik, 2003) and demonstrated empirically (Schnoell, 2014). This effect is likely to be amplified if combined with an attentional bias toward the behavior of group members. Callitrichids seem to indeed perform particularly well in social learning tasks, compared with their closest sister taxa that do not engage in extensive levels of allomaternal care (reviewed in Burkart & van Schaik, 2010, 2016). For instance, a higher proportion of studies found positive evidence of social learning for callitrichids than for capuchin and squirrel monkeys (Custance, Whiten, & Fredman, 2002), and among primates, only callitrichid monkeys have been reported so far to learn about food aversion (Snowdon & Boe, 2003). This increase in performance does not necessarily imply better social learning abilities per se. In fact, it is more likely to arise simply because basic cognitive mechanisms for social learning that are present in many species are applied in species-specific ways, with a bias toward cooperatively breeding primates due to their higher social tolerance and inclination toward relaxed social monitoring (see also Burkart, 2009; Burkart & Finkenwirth, 2015).

Likewise, the strongest evidence for teaching among nonhuman primates can be found among callitrichids, presumably because their prosocial tendency to share food also extends to sharing information (reviewed in Burkart & van Schaik, 2010, 2016). Ideally, these patterns will be confirmed by broad phylogenetically controlled analyses over a large number of species, similar to the approach taken for proactive prosociality and social tolerance. Furthermore, the inclusion of nonprimate species will allow for the identification of how widespread such cognitive consequences of allomaternal care are.

It is important to stress that the strong performance of cooperatively breeding monkeys in social

learning and other sociocognitive tasks is unlikely to be the result of particularly powerful, novel cognitive mechanisms. Rather, it is due to small motivational changes that define how and when cognitive mechanisms that are widespread in nonhuman primates are applied (for a more detailed discussion, see Burkart, 2009; Burkart & Finkenwirth, 2015).

An integrated perspective on cognitive evolution. Recent advances in the understanding of how brains and intelligence evolve have confirmed that social benefits are an important driver of brain size evolution. Nevertheless, they are not the only player in the game and need to be considered in concert with other nonsocial benefits, costs, and factors that modulate the balance between the costs and benefits.

The energetic costs require individuals to mobilize additional resources that can be allocated to the brain, whereas life history costs prevent lineages from evolving a bigger brain if they cannot afford to slow down the pace of their life history (the life history filter). However, if life histories slow down too much, the demographic viability of populations is jeopardized.

The balance between cost and benefits can be modulated via mechanisms of cultural intelligence and cooperative breeding. Cultural species that systematically engage in social learning will gain greater fitness benefits from the same amount of brain tissue, and the net benefits are therefore more likely to exceed the costs in these species. Cooperative breeding alleviates the energetic costs, in particular for maturing individuals who receive energy subsidies from allomothers. Allomaternal contributions also lift the load off mothers, who therefore can invest more, resulting in additional offspring (and thus increased reproductive rate), in brainier offspring, or both. Finally, cooperative breeding, at least in primates, requires high social tolerance and proactive prosociality to work smoothly. These motivational predispositions can facilitate performance in sociocognitive tasks, and in particular social learning. This improved performance does not need to be underpinned by additional or particularly demanding cognitive abilities, but rather results from a different deployment of cognitive abilities

(e.g., for social learning) that are widespread. Once in place, this propensity toward social learning feeds back into cultural intelligence.

It is important to stress that cultural learning and cooperative breeding are not simply other social benefits that drive brain size evolution. In particular, animals must not evolve a bigger brain to be able to become a cooperative breeder. However, everything else being equal, cooperative breeders, as well as species who engage in social learning, should be more likely to respond with brain enlargement to social and ecological cognitive challenges.

IMPLICATIONS FOR HUMAN SOCIALITY AND COGNITION

Humans stand out among primates, with regard to both their hypersociality and their cognitive abilities. Humans stand out among not only primates but also great apes, who as a group have bigger brains than monkeys. Whereas nonhuman great apes occupy a rather similar ecological niche and show rather homogeneous cognitive abilities and brain sizes, humans have evolved much bigger brains, and in contrast to the other great apes, their subsistence ecology is organized around a lifestyle based on intense cooperation, high levels of allomaternal care, cooperative hunting of large game, delayed processing and sharing of meat, and skill-intensive extractive and processing techniques. This lifestyle

is built on unusual cognitive abilities and elaborate cumulative culture and language (see Chapter 14, this volume and Volume 2, Chapters 19 and 20, this handbook). In this final section, I explore to what extent the specific case of humans can be understood as the result of primate-general regularities, or to what extent uniquely human evolutionary processes may be required (see Table 13.2; see also Burkart et al., 2009; Isler & van Schaik, 2014).

First, with regard to the energetic costs related to the evolution of larger brains, this development is likely to have been facilitated through the energy subsidies to immatures. Among mammals, the amount of allomaternal care is most strongly associated with bigger brains in carnivores. Cooperatively breeding carnivores tend to also be cooperative hunters. Arguably, a high-quality diet such as meat allows for more substantial provisioning; furthermore, it provides not only immatures but also adults with more energy. Whether cooperative hunting or cooperative breeding was initially more important to cover the energetic costs of brain enlargement during human evolution is difficult to decide. However, it is telling that chimpanzees, who occasionally also hunt cooperatively, do not use the meat to provision their offspring but rather share it strategically with important social partners. This could suggest that cooperative breeding came first, and after it had installed a psychology grounded on sharing food and perhaps information, cooperative hunting

TABLE 13.2

Overview of How General Primate Trends Coincide and Interacted With the Condition of Our Hominin Ancestors in Different Domains

Domain	How general primate trends could shape the human condition
Energetic costs	<i>Cooperative breeding</i> : energy subsidies from allomothers <i>Cooperative hunting</i> : energy subsidies more substantial, high-quality diet also improves adult energy input
Life history costs	<i>Ancestral condition</i> : large bodies, slow life history, low extrinsic mortality → enables further slowdown
Demographic costs	<i>Cooperative breeding</i> : increased reproductive rates enable breaking through gray ceiling
Cognitive consequences	<i>Ancestral condition</i> : strong social and nonsocial cognitive abilities, often predominantly used in competitive contexts; strong reliance on social learning <i>Cooperative breeding</i> : motivational changes toward higher social tolerance and proactive prosociality result in the deployment of preexisting cognitive abilities in more cooperative context; allows for the emergence of shared intentionality and its cascading effects on cognition <i>Cultural intelligence effects</i> : amplified due to psychological consequences of cooperative breeding, leading to uniquely human adaptations for improved social transmission via cultural group selection

became more important. Perhaps it is most parsimonious to assume that the two coevolved, in that cooperative breeding facilitated the coordination necessary for cooperative hunting and subsequent sharing, and cooperative hunting favored more intense allomaternal care because meat is arguably much more suitable than plant matter for substantial provisioning.

Second, our hominin ancestors were large-bodied primates with slow life histories, and due to their body size they were less vulnerable to predation than smaller bodied primates. They thus met essential preconditions for a further slowdown of their life history. Third, with regard to demographic costs, the problem is that if brains grow too large over evolutionary time, life history would have to slow down to the extent that demographic viability is no longer warranted because of insufficient reproduction rates. Thus, a species can increase its brain only to the size at which the decrease in reproduction rate still allows for sufficient population stability. For great apes, including humans, a conservative estimate of this so-called gray ceiling is 600–700 cm³, which is far exceeded by modern human brains (Isler & van Schaik, 2012b). The explanation for why humans but none of the other great apes could break through the gray ceiling without going extinct is that allomaternal care allowed for higher female reproductive rates despite the slow life history, corresponding to the life history pattern present in other cooperatively breeding mammals and primates.

Finally, we can examine the implications from a more psychological point of view. Comparative data have suggested that our great ape-like, big-brained ancestor had strong social and nonsocial cognitive abilities, comparable to extant great apes. As in extant great apes, these skills were often predominantly used in competitive contexts. When this ancestor started to engage in cooperative breeding during the Pleistocene, its mind was complemented with more tolerant and more prosocial psychological predispositions. These motivational changes may have resulted in the deployment of preexisting cognitive abilities in more cooperative contexts, perhaps most importantly allowing for the emergence of shared intentionality and its cascading effects on cognition (Burkart et al., 2009).

Shared intentionality has been put forward as the key difference between ape and human cognition by transforming great ape cognitive skills into typically human forms and enabling children to participate in cultural practices and ontogenetically construct the full range of human cognitive abilities (Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Finally, improved social transmission is likely to have rendered the mechanisms of cultural intelligence in the broad sense more powerful as well as to have paved the way for uniquely human evolutionary processes such as cultural group selection, which are arguably needed to understand how small-scale societies in prehistoric times could evolve into larger and more complex societies during the Holocene (Richerson et al., 2016).

In sum, we can see that part of the answer to what makes humans unique may be our exceptional blend of talents: those inherited through common descent from our great ape-like ancestors and those that were added convergently and are derived relative to other great apes, as a consequence of the fact that sometime during the Pleistocene our ancestors had started to raise their children together. More broadly, I thus argue in this chapter that primate-general regularities applied to the specific case of humans seem to have ample explanatory power and that uniquely human evolutionary processes are necessary only at a late stage. The fine print of the primate-general regularities outlined in this chapter is still full of knowledge gaps, and broad phylogenetic analyses are needed to confirm emerging trends.

An obvious question is to what extent cultural intelligence and cooperative breeding also play a role in cognitive evolution in lineages other than that of primates. Empirical data are largely missing to date to test the respective predictions as has been done for primates. Nevertheless, one could argue that cultural intelligence effects in the broad sense should be expected in a variety of lineages that engage in social learning (i.e., that ontogenetically, an increase in opportunities for social learning results in larger adult skill sets and that, evolutionarily, species who rely more systematically on social learning are more likely to evolve a bigger brain). Effects of cooperative breeding, however, may show higher variability, depending on the form of help provided by helpers.

For instance, fish helpers may fan eggs or defend the territory (Taborsky & Limberger, 1981), which, unlike the food sharing, provisioning, and infant carrying typical of primate helpers, is unlikely to require high levels of social tolerance and proactive prosociality or provide energetic benefits. Nevertheless, provisioning is arguably the most widespread alloparental behavior in most lineages, and it may very well result in convergent consequences across lineages.

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