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**ARTICLES**

# Cooperative Breeding and Human Cognitive Evolution

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Despite sharing a recent common ancestor, humans are surprisingly different from other great apes. The most obvious discontinuities are related to our cognitive abilities, including language, but we also have a markedly different, cooperative breeding system. Among many nonhuman primates and mammals in general, cooperative breeding is accompanied by psychological changes leading to greater prosociality, which directly enhances performance in social cognition. Here we propose that these cognitive consequences of cooperative breeding could have become more pervasive in the human lineage because the psychological changes were added to an ape-level cognitive system capable of understanding simple mental states, albeit mainly in competitive contexts. Once more prosocial motivations were added, these cognitive abilities could also be used for cooperative purposes, including a willingness to share mental states, thereby enabling the emergence of shared intentionality. Shared intentionality has been identified as the original source of many uniquely human cognitive abilities, including cumulative culture and language. Shared intentionality rests on a fundamentally prosocial disposition that is strikingly absent in chimpanzees, but present in cooperatively breeding primates. Thus, our hypothesis is that while chimpanzees and perhaps all great apes exhibit many of the important *cognitive* preconditions for uniquely human mental capacities to evolve, they lack the *psychological* preconditions. In humans, we argue, the two components merged, the cognitive component due to common descent from ape ancestors and the motivational component due to convergent evolution of traits typical of many cooperative breeders.

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As recently as 6 to 7 million years ago, the hominin lineage split off from the rest of the great ape (hominid) lineage[1] and consequently shares many biological traits and behavioral and cognitive similarities with great apes.[2,3] Nevertheless, humans also exhibit remarkable differences from our closest relatives. First, we not only live far longer lives and reproduce at faster rates than do the other great apes, but our offspring take much longer to mature and women cease reproduction well before somatic senescence sets in.[4] Second, our ecological niche involves specialization on large, valuable food packages that have to be acquired together, as well as shared, and mandatory reliance on techniques acquired through cumulative culture.[5] This niche and our social relationships are based on an un-apelike selflessness, a degree of hypersociality reflected in a concern for others, eagerness to share food and information with others, and cooperation in a wide array of contexts, even with nonrelatives and near-strangers.[5–8] Our mode of life facilitates our spread into new habitats, resulting in a ubiquitous geographic distribution.[9] Third, with regard to intellectual performance, humans differ from the other great apes, which, as a group, show relatively homogeneous cognitive abilities.[10–12]

Whenever a species exhibits multiple derived traits, it may be helpful to begin by asking if these are causally connected. Many anthropologists have argued that humankind's peculiar package of traits coevolved with the rise of the genus *Homo* around 2 Ma,[5,13] which supports the possibility of a causal connection. The cooperative breeding hypothesis claims that the emergence in the genus *Homo* of allomaternal care and provisioning of young by a range of helpers accounts for many of these species-specific traits.[9,14,15] The life-history, ecological, and demographic dimensions of the cooperative breeding hypothesis are beginning to be well documented, but much less work has been done on developing the psychological and cognitive dimensions of the model, particularly as they apply to allomothers. While Hrdy[9,14,16] has explored the emotional implications for children and mothers, she has glossed over the cognitive implications for allomothers, our main focus here. By extrapolating from the general pattern of psychological consequences of cooperative breeding in other taxa,[17] we elaborate the role of this breeding system in the emergence of uniquely human cognition.

## GLOSSARY

***Allomaternal care***—care for immatures by individuals female or male group members other than the mother, including, in many cases, care by the genetic father. Ideally, the term is reserved for those cases in which paternity is known, as in strictly monogamous breeding systems or ones where DNA data are available.

***Cognitive performance versus cognitive potential***—the distinction between cognitive performance and ability refers to the cognitive potential inherent in an organism (ability) and its actual implementation in real-life problem-solving situations (performance), Performance can be reduced relative to potential by various factors. A well-known discrepancy between performance and potential occurs in social learning, where social dynamics can inhibit performance even if individuals would, in principle, be able to perform it.[80] Cooperative breeding removes restrictions on performance in many ways,[17] making it likely that increased performance in socio-cognitive contexts in cooperatively breeding primates, compared to their independently breeding sister taxa, is not necessarily linked to greater cognitive potential or ability *per se*.[26]

***Cooperative breeding & independent breeding***—breeding systems can be described along a gradient that specifies who is responsible for infant care. At one end of this continuum, we have independent breeders with exclusive maternal care. Typical cases include chimpanzees or orangutans. The mother is very possessive of her infant. Although she may allow male or female group members (allomothers) to touch or handle (but not remove) her infant, for at least the first six months. she resists all attempts by others to take or carry her infant. In species with exclusive maternal care, allomothers can take infants only under unusual circumstances, as when the mother is incapacitated or a dominant female "kidnaps" her infant. Cooperative breeders fall at the other end of the continuum, where mothers voluntarily permit access to their infants and many group members are actively engaged in active care and provisioning of infants, thereby increasing their growth and survival.

***Cultural intelligence***—in its broad version,[83–85] the cultural intelligence hypothesis seeks to explain why species engaging in social learning are more likely than others to evolve large brains. It proposes that optimization of social learning favors the evolution of larger brains and increased general cognitive potential because organisms capable of social learning can more easily respond to selective pressures to enhance cognitive skills and brain size. Because social guidance improves the signal-to-noise ratio in available environmental inputs necessary for brain development relative to individual exploration and learning as required for individual skill acquisition, the efficiency with which brain tissue can generate adaptive cognitive skills can thus be increased if skill acquisition is socially guided. The human version of the cultural intelligence hypothesis refers to the process whereby our species-typical socio-cognitive abilities, (including shared intentionality) which emerge and develop in early childhood, triggers the emergence of uniquely human cognition.[12]

***Prosocial behavior***—behaviors that produce benefits to others. At the proximate level, such behaviors can be motivated by impulses to help others (spontaneous prosociality), but they can also result from other psychological processes, such as the calculation of one's own future benefits by calculated reciprocity, enforcement by the recipient through harassment or intimidation or, more subtly, be elicited by tolerated theft and begging by the recipient and high social tolerance for these activities by the donors.

***Spontaneous prosociality***—refers to a motivational predisposition to perform acts that benefit others, even in the absence of the expectation of reciprocation and solicitation by the recipient, such as begging and harassment. Importantly, such spontaneous prosociality is more than a quantitative extension of social tolerance, which is a permissive, but passive attitude towards various behaviors of social partners. This is because prosociality crucially includes a motivational drive actively to affect others' circumstances in a positive way, a spontaneous helping impulse that does not have to be elicited through external signals like begging. Spontaneous prosociality corresponds to the concept of "other-regarding preferences" commonly invoked by economists to describe behavioral outcomes that are not only motivated by the maximization of one's own benefits, but also increases benefits to others.[7]

***Shared intentionality***—refers to the "ability to participate with others in collaborative activities with shared goals and intentions" along with the desire to do so.[22:675] This capacity emerges much earlier during human ontogeny than does a fully fledged theory of mind, but its routine expression is strikingly absent in other apes.[12] It is based on a *cognitive* component, or the understanding of others, goals and intentions, and on a *motivational* component, the desire to do this. In a proposal central to this paper, Tomasello and Carpenter[25] specified how shared intentionality is crucial in transforming the basic understanding of other minds, as found in great apes, into joint attention, cooperative communication, collaboration, and instructed learning. These, in turn, give rise to further cognitive developments, for example by cultural construction,[113,128] but also by releasing co-evolutionary processes between social and nonsocial cognitive abilities whereby the increased efficiency of brains due to social learning also facilitates the development and evolution of nonsocial cognitive abilities (see also "cultural intelligence").[85]

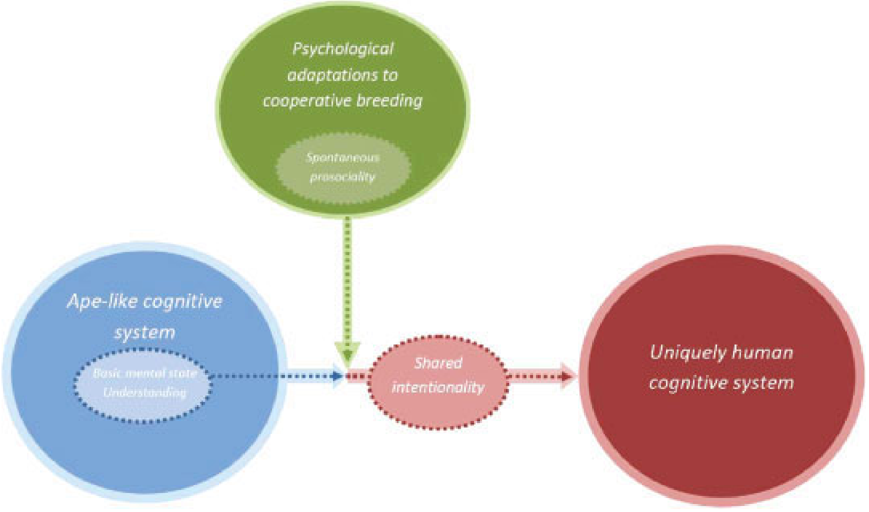

Figure 1. The role of cooperative breeding in the transition from ape-like to uniquely human cognition. In many species, engaging in shared care plus provisioning is likely to be accompanied by psychological adaptations such as increased social tolerance and spontaneous prosociality. These can increase cognitive performance in the social domain, as seen in callitrichids. In humans, however, spontaneous prosociality was added to an already ape-like cognitive system, among others capable of basic mental state understanding. In addition to the cognitive consequences observed in other cooperatively breeding species, this enabled the emergence of shared intentionality. Shared intentionality (see glossary) has been identified as a key difference between humans and other great apes; it is responsible for the emergence of uniquely human cognitive systems both phylogenetically and ontogenetically.[22] (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

Before we can explain the cognitive evolution of the human lineage, we have to identify the cognitive differences between humans and the other apes. While earlier accounts have often stressed the key role of theory of mind,[18–20] more recent results suggest that apes do have simple elements of that theory, such as an emerging understanding of what others are attending to and intending, although these capacities are primarily expressed in competitive contexts[11] (but see Penn and Povinelli[21]). Such findings shift the focus onto the apparently central role played by shared intentionality,[22,23] which has now been identified as the fundamental source for the majority, if not all, of our unique cognitive achievements. Those include language, complex technologies, and art, as well as formalized norms and institutions, which in turn gave rise to religion. These achievements permit the formation of large, structurally complex societies, such as states.[23–25]

The crucial question is therefore what precipitated the evolution of shared intentionality. Shared intentionality is critically based on a prosocial motivational predisposition that involves an interest in sharing psychological states with others.[22] The rudimentary understanding of psychological states in apes seems to be restricted to competitive contexts,[11] not cooperative contexts. Hence, the precondition for shared intentionality that apes lack is not the capacity to grasp mental states *per se*, but the motivational predisposition actively to share mental states with others, to care about others' mental states, and thus to use mental state understanding systematically in cooperative contexts.

These findings indicate that discovering what really made us human largely boils down to answering the question of what was responsible for the evolution of such fundamentally prosocial attitudes. Based on comparative data suggesting that cooperative breeding plays a central role in the evolution of prosociality (Box 1), we argue that engaging in routine allomaternal care and provisioning was the impetus behind the emergence of prosocial dispositions and thus, eventually, uniquely human cognition (Fig. 1). Hence, we will first briefly summarize the psychological and resulting cognitive consequences of cooperative breeding based on studies of nonhuman primates and other mammals (reviewed elsewhere in detail[17,26]). We will then return to the specific human case by asking readers to engage in a thought experiment: What happens if we take a clever ape with incipient tool manufacturing and tool using potentials, rudimentary theory of mind, and some empathic capacity, then introduce cooperative breeding, a novel mode of child-rearing? We conclude by proposing a set of predictions and steps required for further testing of these ideas.

## THE PSYCHOLOGY OF COOPERATIVE BREEDING

Broadly defined, cooperative breeding refers to any breeding system in which individuals other than parents (alloparents) help to care for and provision offspring.[27,28] Some researchers require that breeding-age helpers temporarily forgo independent reproduction,[29,30] as has been argued to be the case among humans (mid-life menopause).[9,31] As will become evident, this point is not relevant to the psychological and cognitive dimension of the cooperative breeding hypothesis elaborated here. The crucial feature here is the availability in the group of a num-

## BOX 1: Spontaneous Prosociality in Nonhuman Primates

Compared to independently breeding primates, cooperatively breeding primates show many more behaviors suggestive of spontaneous prosociality in naturalistic situations, in particular unsolicited food offering. Experimental evidence supports this pattern: Direct tests for spontaneous prosociality were positive for cooperatively breeding primates (tamarins[42,43] but see[73] and marmosets[45]) but not for independently breeding primates (chimpanzees[55–57,74] and macaques[58–60,61]), with capuchin monkeys being intermediate in both allomaternal care[62–66] and prosociality.[67,68]

Nevertheless, some species with exclusive maternal care, such as bonobos and chimpanzees, cooperate to some degree, both in the wild and in captivity. Based on evidence available to date, we think it likely that such cooperative and altruistic actions on the part of independent breeders are regulated by different psychological mechanisms, including self-interest,[75] the expectation of reciprocation,[48,51,76] the combination of solicitation by one partner and high social tolerance by the other (for example in food sharing[77]), or cognitive empathy in response to signs of need.[74,78] However, the case is still open. Further, truly comparable studies are necessary. However, if spontaneous prosociality is present in independent breeders such as chimpanzees, we predict that it will occur in limited contexts and involve a small set of partners with whom the animals have strong social bonds[47] because naturalistically occurring altruistic and cooperative behaviors are also restricted to such dyads[76] or to contexts not directly involving food.

The mismatch between laboratory experiments and some albeit not most naturalistic observations suggests that we should be cautious about extrapolating from behavior to motivations. As de Waal[79:47] specifically reminds us in the case of animal empathy, "it is not enough to review the highlights of succorant behavior, it is equally important to consider the absence of such behavior when it might have been expected." More fundamentally, the presence of cooperative behavior *per se*, (such as targeted helping) does not allow inferences about the proximate psychological mechanism motivating it. In order to demonstrate that targeted helping is driven by spontaneous prosociality and thus is unsolicited, intrinsically motivated helping rather than response to signals of need, we need to exclude alternative possibilities, such as the expectation of reciprocation and, most importantly, responding to direct solicitation, as was shown for marmosets.[45] Nevertheless, for the moment we cannot rule out the possibility that in some contexts and under some conditions, behaviors of independent breeders like chimpanzees express prosocial tendencies.[74]

Yet, on current evidence, both from the wild and captivity, substantial differences between callitrichids and independently breeding primates persist, particularly with regard to the range of recipients toward whom these behaviors are directed and the strength of altruistic behaviors (Fig. 1). First, the range of recipients of prosocial acts was larger and less selective in callitrichids. Prosocial acts were no stronger toward preferred social partners or close kin than toward nongroup members.[45] Indeed, callitrichid society is characterized by strong social bonds among all group members. Privileged relationships within specific dyads are rare and hard to detect.[39,40] In contrast, in both chimpanzees and capuchin monkeys, altruistic acts are typically limited to close friends and bonded kin or depend on dominance. Experimental evidence regarding these monkeys is drawn from preselected subjects for which it was known in advance that they would be particularly prone to pay attention to a partner [67] or that had been successful in cooperating in previous tests.[74] Moreover, the strength of prosociality is strongest in callitrichids. In food contexts, common marmosets perform altruistic acts even at some cost without deriving a benefit for themselves at all,[45] while capuchin monkeys cease their prosocial behaviors under unequal reward distributions[67,68] and chimpanzees fail altogether to show altruistic tendencies.[55–57,74]

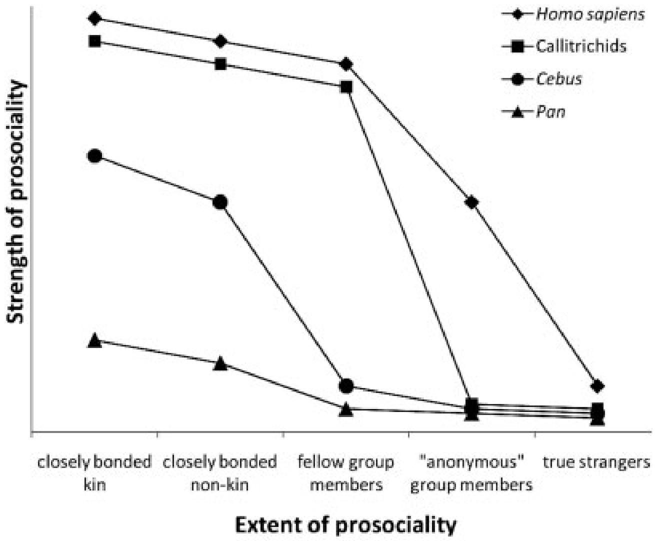

Figure 1. Across primates, prosociality varies in *intensity* (strength) and *extent* (range of recipients). These contexts, in turn, depend on additional, mostly cognitive preconditions, (see text). Compared to other primates, humans have an additional class of potential recipients of prosociality; these are unrelated, perhaps even never-before-encountered group members, who are part of the larger community but not the local group.

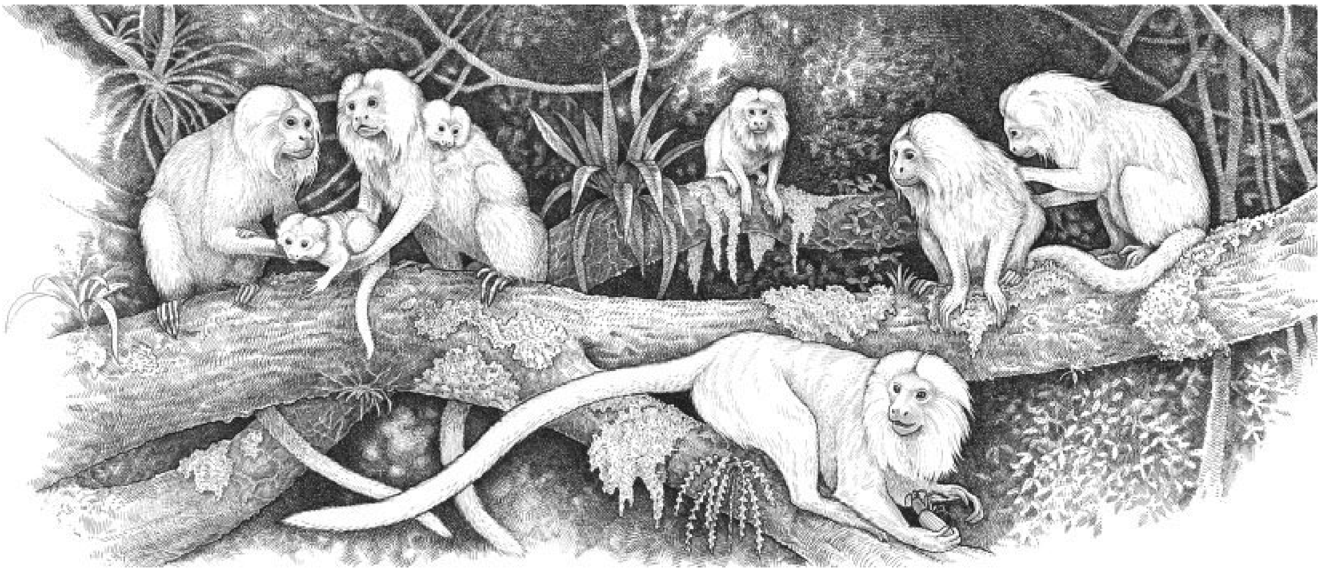

Figure 2. A family group of cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*). Females can give birth to twins twice a year without experiencing lactational amenorrhea. The mother can afford this high energetic investment because the infants are carried, and after weaning, provisioned by all group members, mostly fathers and older siblings, but also nonrelatives. Drawing by Sarah Landry.

ber of reliable helpers. Among primates, allomaternal care, whereby group members other than the mother protect, keep warm, or otherwise care for the young, is widespread. However, the strongest reliance on allomaternal care and provisioning is found in humans and callitrichids, where many group members contribute to infant-rearing.[9]

Callitrichid monkeys, (marmosets and tamarins),[32] live in family groups typically composed of a single breeding pair and its adult and immature offspring, although polygynous and especially polyandrous constellations occur as well.[33] Helpers tend not to be reproductively active in the group. All group members, including unrelated or even initially unfamiliar individuals,[34] systematically engage in many cooperative behaviors, ranging from infant carrying, shared vigilance, and systematic provisioning with high-value food items to collective action such as communal group defense (Fig. 2).[32,35] Zahed and coworkers[36] demonstrated that adult male marmosets in general possess a spontaneous motivation to care for any infant, related or not. Helpers often provision offspring by giving food calls and actively offering high-value food items rather than in response to infant begging.[37] Callitrichid infants spontaneously transfer to allomothers. This is unusual among primates and suggests that there has been a sufficiently long history of benevolent attention and effective allomaternal care to produce selection for this self-transfer by infants. Allomothers, meanwhile, never forcefully retrieve an infant from another helper or the mother. Rather, transfers occur in a highly orchestrated manner, indicating that each caretaker's behaviors and intentions are continuously monitored and their behaviors are adjusted accordingly. Finally, callitrichids show high levels of social tolerance (Fig. 3), are highly responsive to signals from other group members,[38–40] and do not appear to punish underperforming helpers.[41] Based on this natural history, one can deduce that callitrichid caregivers have spontaneously prosocial motivations that render them eager to perform acts that benefit others, even in the absence of either solicitation by the recipient, (such as begging or harassment), or expectation of reciprocation.

Experimental tests show that cotton-top tamarins[42–44] and common marmosets[45] have a spontaneous helping impulse when they are given the opportunity to provide food to group members, even if they don't receive anything for themselves if recipients cannot reciprocate, and in the absence of begging. Moreover, prosocial food donations in the marmoset experiments were not exclusively directed at infants or other immatures but to any group members; equally strong toward relatives as to unrelated group members or unrelated potential group members; not solicited by the recipients; and not selectively directed at preferred social partners. If spontaneous prosociality were to occur in any primate with more nearly exclusively maternal care of young infants, we would expect it among species such as bonobos, chimpanzees, or capuchins, since all three occasionally share food and exhibit more cooperative and altruistic behaviors than is typical of most primates.[46–49] However, their food sharing is usually preceded by begging or resembles tolerated taking.[49–52] Bonobo allomothers very occasionally allow immature individuals to take vegetable food or meat, and in rare instances offer it.[46,53] Among chimpanzees, even food sharing between mother and infant resembles tolerated theft. Rare cases of donation typically involve low-value food items or discarded remains such as nonedible husks and only occur after begging by the infant.[54] The infrequent and often grudging nature of these food deliveries differs from the spontaneous, unsolicited, and routine offering of high-value food that is observed among callitrichids and humans, including children.[37] In accordance with these differences, experiments have so far failed to show evidence of prosociality in species with exclusive maternal care

Figure 3. Common marmosets (*Callithrix jacchus*). A sexually mature helper watches how another adult processes an unusual food. Relaxed, close monitoring of each others' activities is not restricted to infant-caregiver dyads. It occurs in all dyad types and in a variety of contexts. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

of infants, such as chimpanzees[55–57] or macaques.[58–61]

Capuchin monkeys show more elements of cooperative breeding than do the *Pan* species, with occasional allomaternal carrying, suckling of older infants between the ages of 3 and 6 months, and low levels of allomaternal provisioning.[62–66] The majority of shared food is transferred from allomothers to immatures. In one-fifth of all 18 observations of food transfer, it was actively offered by one monkey to another. Half of these involved offerings by nulliparous females to infants[49:740]. On rare occasions, food is actively shared between adults.[52] Indeed, experiments suggest some prosociality among capuchins.[67,68] A broader discussion is provided in Box 1.

Some canids, elephants, and other nonprimate cooperative breeders exhibit similar natural history, suggesting analogous prosocial motivations.[17] Spontaneous prosociality is suggested by a variety of behaviors of African wild dogs (*Lycaon pictus*). These include spontaneous provisioning through regurgitation and, less often, the carrying of carcass portions back to the den to provision pregnant and lactating mothers or babysitters as well as pups. In addition, pups enjoy feeding priority. Such extreme allomaternal investment is not the result of coercion. Indeed, it is not even restricted to closely related pups, underscoring just how intrinsic motivations to nurture and provision are. Canid prosocial care even extends to adult group members, as suggested by tolerance at kills and cases in which incapacitated and older pack members are provisioned by others. Similar results are reported for elephants among which allomaternal care improves calf growth and survival.[17] Thus, although no experiments have been conducted yet, the natural history of these nonprimate cooperative breeders suggests the presence of a similar helping impulse.

When such spontaneous prosociality extends from the donation of food to that of information, we enter the realm of teaching. As Rapaport emphasized,[69] teaching, which is rare in nature, is strikingly overrepresented in species relying on cooperative breeding; positive evidence is limited to ants, pied babblers, meerkats, callitrichids, and solitary felids.[69] Thus, teaching is limited to species showing unsolicited food donation, and hence is overrepresented among cooperative breeders.[70] Its presence in independently breeding feline carnivores derives from the need to provision offspring who require much time to learn to capture their own prey.[71] Despite the impressive socio-cognitive potential of nonhuman apes, such as simple mental state attribution,[72] it is worth noting that comparable observations of teaching are not reported for these taxa.

In sum, in nonhuman primates, canids, and elephants, cooperative breeding is associated not only with increased levels of social tolerance and responsiveness to the signals and needs of others, but also with the presence of spontaneous prosocial motivations, which extend beyond infants and sometimes beyond food to information, resulting in teaching.

## COOPERATIVE BREEDING AND COGNITION

There is no *a priori* reason why cooperative breeders would require greater cognitive skills than do other species. However, cooperative breeding seems to result in increased cognitive performance as a side effect.[9,16,38] Indeed, a comparison[17,26] of callitrichids and their more independently breeding sister taxa, capuchin and squirrel monkeys, in their performance on cognitive tasks found that callitrichids systematically outperformed their sister taxa in the social domain, but scored lower in nonsocial cognitive tasks (Table 1). These effects, however, need not reflect fundamentally enhanced cognitive ability. Instead, they are more likely the result of motivational changes associated with cooperative breeding.[26] Social learning, for example, which has been documented more consistently in primates that

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**TABLE 1. Cognitive Domains in Which Cooperatively Breeding Callitrichids Do or Do Not Outperform Their Independently Breeding Sister Taxa**[a]

| *Increased in cooperatively breeding primates* | *Not increased in cooperatively breeding primates* |
|---|---|
| Socio-cognitive abilities | Nonsocial cognitive abilities |
| • Social learning | • General cognitive ability |
| • Vocal communication | • Working memory of actions |
| • Teaching-like behaviors | • Innovation rates |
| • Gaze understanding | • Tool-use rates |
| • Cooperative problem solving | • Patience |
|  | • Inhibitory control |

[a] For a full description, see Burkart and van Schaik.[17]

breed cooperatively than in primates that do not, is well known to depend not only on the cognitive skills involved, but at least as much on the level of social tolerance.[80] Such tolerance facilitates close-range attention to conspecific behavior and even permits mutual gazing without provoking attack (Burkart, unpublished; personal communication from Karen Bales). Indeed, even if the cognitive prerequisites for imitational learning are present in other monkey species,[81,82] their application to imitative learning may be hampered by a lack of mutual tolerance.[26] Thus, the more effective performance of cooperative breeders in socio-cognitive tasks is likely to be a side effect of motivational changes directly related to the deployment and coordination of caregiving activities,[17] as well as a side effect of developmental adjustments by immature individuals, who must monitor the whereabouts and intentions of their mother and allomothers.[9,16]

Cooperative breeding may also remove obstacles to the evolution of brain size. First, because social learning enhances the efficient use of brain tissue, a social system with increased opportunities for social learning can, over evolutionary time, favor the evolution of larger brains, as detailed in the general version of the cultural intelligence hypothesis.[83–85] This hypothesis predicts that many cooperative breeders have evolved larger brains than have their independently breeding counterparts. Second, Isler and van Schaik[86,87] have shown the existence of a maximum sustainable brain size in a given lineage. This “gray ceiling” is a result of a strong reduction in maximum reproductive rate due to increased brain size (principally as a consequence of delayed maturation).[88] However, these researchers also found that this rule does not hold among cooperative breeders, probably because energy inputs to mothers and newly weaned infants from allomaternal provisioning allows these species to escape from under this so-called gray ceiling and thus evolve larger brains.

These kinds of effects may explain why cooperative breeding is linked not only to psychological dispositions, but also to cognitive performance in primates and other mammals. Although details of cooperative breeding systems are bound to differ between taxa depending, for example, on the degree of reproductive skew or presence of nonkin, other cooperatively breeding mammals, such as canids and elephants, show similarly strong socio-cognitive performance without a concomitant increase in nonsocial cognitive tasks.[17] The socio-cognitive performance of elephants parallels the callitrichid pattern. With the exception of their memory capacity, their performance in many nonsocial cognitive tasks is unimpressive for a mammal with such a large brain, yet they excel in socio-cognitive contexts, including mirror self-recognition and vocal imitation.

Recent experiments with dogs have revealed socio-cognitive performances that rival those of apes. These include the understanding of visual perspective and mental states, victim-directed third-party postconflict affiliation (“consolation”), reasoning by exclusion in a social context, sophisticated passive and active communicative abilities, cooperation skills, and imitation, including selective inferential imitation. Yet in the nonsocial and physical realm, dogs perform less impressively than do great apes. However, such studies are rare and thus difficult to evaluate.[17] Superior socio-cognitive performance in dogs cannot be explained by domestication alone[89,90] since comparable effects are not found in other domesticated animals except those that are also cooperative breeders. For example, rapid experimentally induced domestication of silver foxes (*Vulpes vulpes*), which also breed cooperatively,[91,92] produced a similar increase in socio-cognitive performance.[93] Thus, socio-cognitive abilities that were already present in wild ancestors are likely to have been amplified and directed by humans through selective breeding, or domestication.

A positive effect of cooperative breeding on inter-individual social tolerance, including maternal tolerance of others postpartum, spontaneous prosociality (the helping impulse) and socio-cognitive performance is well documented for nonhuman primates and likely for other taxa. An extrapolation of these general findings to the hominin lineage suggests that humans also fit this pattern.

## COOPERATIVE BREEDING AND THE EVOLUTION OF HUMAN COGNITION

Given the motivational and cognitive consequences of cooperative breeding in other taxa what might have happened when our ape-like ancestors adopted such breeding system? We can extrapolate from the comparative findings and provide a first, tentative sketch of how this new mode of childrearing could have led to key features of uniquely human cognition. Fitting the general pattern, humans clearly show the psychological dispositions associated with cooperative breeding, particularly strong social tolerance and spontaneous prosociality. The cognitive differences between our great-ape like ancestors and ourselves, however, are far more pervasive than those between callithrichids and their sister taxa. We argue that the cognitive consequences of cooperative breeding were more pronounced in our ancestors than in other taxa because the selection pressures associated with cooperative breeding were acting on an already ape-like cognitive system, allowing for the emer-

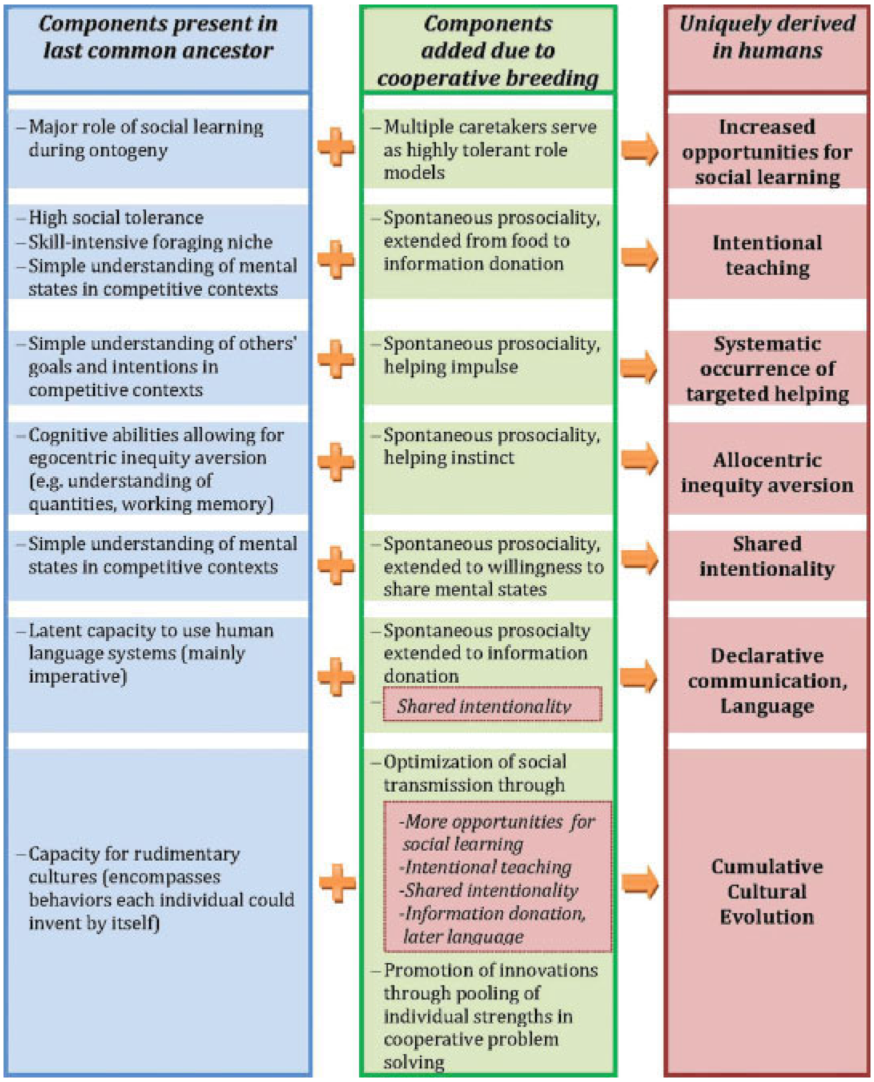

Figure 4. Origin of key components of uniquely derived human cognition as elaborated in the text. The components highlighted in *italics* indicate sequential evolutionary processes further specified in the text. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

gence of shared intentionality (Fig. 1).[22] Our hypothesis is that while chimpanzees and, perhaps, all great apes[10,11] may have many of the relevant cognitive preconditions for uniquely human cognition to evolve, they lack the motivational preconditions. In humans alone, these two components have come together, the cognitive component due to common descent and the motivational component due to convergent evolution resulting from the selection pressures associated with cooperative breeding (Fig. 4).

Understanding the role of cooperative breeding in the emergence of human cognition first requires that we delineate the point of departure; that is, the cognitive system that was in place when the selection pressures of cooperative breeding were added during human evolution. Because cooperative breeding arose after the split between hominins and great apes, a conservative estimate of the cognitive endowment of the hominin that first adopted cooperative breeding would be that it was rather similar to that of the last common ancestor. Given the cognitive similarities among great apes, we postulate that the cognitive potential for early hominins was similar to that of extant great apes; that is, more complex than the cognitive potential of monkeys in both social and nonsocial domains.[10,11,94]

Two consequences follow directly from adding cooperative breeding to such a cognitive system. First, existing *cognitive skills become available for deployment in cooperative contexts*. In the nonsocial domain, cognitive performance tends to be more pronounced in great apes than in other nonhuman primates as shown by a meta-analysis based on a variety of tasks such as learning sets, patterned-string problems, reversal learning, delayed response, and invisible displacement.[10] Great apes also use tools more often,[95] do so based on causal understanding,[96,97] and plan ahead by anticipating their future needs, such as need for a tool.[98,99] Such skills, in particular simple planning, can greatly improve the coordination of activities among group members. Second, cooperative breeding amplifies *opportunities for social learning*. Immature individuals in cooperatively breeding species have increased opportunities for social learning because of the availability of multiple, highly tolerant role models, as well as potentially longer juvenile learning periods,[16,100] thus expanding individual skill repertoires.

**Our hypothesis is that while chimpanzees and, perhaps, all great apes may have many of the relevant cognitive preconditions for uniquely human cognition to evolve, they lack the motivational preconditions. In humans alone, these two components have come together...**

Such immediate consequences can also occur in other cooperatively breeding species, but will be less pronounced because ape-level cognitive potential was not present to begin with. Thus, the cognitive consequences to be discussed could have emerged only in humans. *Intentional teaching* requires an understanding of another individual's knowledge state.[101,102] Such an understanding is present in great apes, but is predominantly restricted to competitive contexts.[11,25,72,103] Furthermore, some understanding of causal relationships in general, which is present and, to all appearances, deeper in great apes than in other primates,[10,97] is an important precondition for the active transmission of more complex skills. However, all these cognitive components will fail to result in intentional teaching unless some willingness to share information is present, a willingness derived from an extension of spontaneous prosociality in food-sharing contexts to information sharing. In humans, sharing information with immature individuals seems to have played a particularly important role, as highlighted by Csibra and Gergely[104] who propose that we have evolved additional adaptations facilitating skill transfer, summarized under the concept of pedagogy.

The sporadic occurrence of targeted helping among chimpanzees underscores their ability to understand the goals, intentions and needs of others.[74,105] Overall, however, targeted helping is rare; it is entirely absent when food is at issue, suggesting that chimpanzees lack any strong motivation to help, even if they presumably understand how their targeted actions could benefit others in specific situations. Adding a helping impulse would further increase the motivation to improve others' situations when preexisting cognitive mechanisms correctly identified that and why an individual is in need of help, thus resulting in the *systematic occurrence of targeted helping*.

Chimpanzees may have the cognitive prerequisites for recognizing inequitable distributions and responding to egocentric or "disadvantageous" inequity if they themselves are affected by unfair offers.[106] However, this issue is controversial.[107] If such a basic ability to detect inequity is coupled with a concern not only for one's own well-being, but also for that of others, egocentric inequity aversion can turn into *allocentric inequity aversion*; that is, antipathy against unfair treatment of others, or at least in-group members.[6]

The rudimentary ability to grasp others' mental states, which has been documented for great apes[72] but not for cooperatively breeding primates (such as marmosets),[108] makes it possible that in humans the helping impulses are no longer confined to food or information, but extend to a willingness to share mental states. This, in turn, enables the emergence of *shared intentionality*, which is critically based on a prosocial motivational predisposition that encompasses an interest in sharing psychological states with others.[22] Shared intentionality is considered to be the basis for many aspects of uniquely human cognition.[25] Through shared intentionality, the adoption of cooperative breeding might have influenced the emergence of an array of other capacities, including language and cumulative cultural evolution. Let us briefly consider these.

**... it is a common notion in linguistic pragmatics that human communication is based on the principle of cooperation. The cooperative breeding hypothesis provides a simple and biologically valid solution to this longstanding problem.**

Experiments with enculturated great apes illustrate that they possess the cognitive capacities for acquiring simple *language* systems.[109] However, the use of such systems among great apes remains predominantly imperative; that is they use their language skills primarily to request things rather than for sharing information with others in declarative modes.[18] The same limitation is apparent in their use of pointing gestures, which are also restricted to imperative contexts.[110,111] The absence of a helping impulse is manifest in this lack of interest in sharing information with others. This strongly contrasts with the way humans use language. Even from a very young age, children use language for declarative purposes.[112] Correspondingly, many developmental psychologists have emphasized the role of joint attention and shared intentionality for language development.[23,113–116]

Any scenario for the evolution of language needs to explain where this fundamental prosocial and cooperative attitude essential for language came from and how it originated. Language could only evolve in a communication system characterized by prosociality and, as Zahavi[117] pointed out long ago, would disappear if cheaters predominated. Indeed, it is a common notion in linguistic pragmatics that human communication is based on the principle of cooperation.[118,119] The cooperative breeding hypothesis provides a simple and biologically valid solution to this longstanding problem. The psychological endowment of cooperative breeders provides precisely the motivational preconditions needed for the evolution of honest, low-cost communication signals.[120]

Finally, shared care and provisioning can have the potential to promote *cultural evolution* in multiple ways. Cultural evolution requires innovations and their subsequent social transmission.[121] While cultural variation in behavior is known in great apes, the contents of these cultures tend to be hardly more complex than what could be independently invented. Moreover, they are only marginally cumulative.[122,123] Compared to other apes, more active, accurate, and reliable transmission of skills and knowledge are favored in humans by increased opportunities for social learning, the presence of intentional teaching, shared intentionality, and declarative communicative activities. It is also conceivable that prosociality promotes innovation, but this topic is as yet largely unexplored. However, the capacity to solve problems cooperatively can result in pooling of individual strengths, particularly when individuals jointly participate with others in collaborative activities with shared goals and intentions.[124]

It is important to note that the transitions we have described are likely to be achieved on a population-wide basis only if the helping impulse, as expressed in willingness to share information or mental states, is also ubiquitous in the population rather than restricted to specific dyads. This could help explain why the unusual cognitive potentials universally present in *Homo sapiens* evolved in a line of cooperatively breeding apes while failing to evolve in independently breeding apes like chimpanzees, no matter how intelligent their ancestors were to begin with.

## FUTURE DIRECTIONS

The cooperative breeding hypothesis is compatible with most other hypotheses for the origin of human uniqueness in that it provides the context in which these various processes could operate (discussed extensively by van Schaik and Burkart[125]). Moreover, it is consistent with our current state of knowledge of the evolution of human derived features. Nonetheless, more rigorous tests are needed of both the broad interspecific version, which requires systematic examination of various predictions of this hypothesis in a broad array of species, and of the specific application to the human lineage.

- Comparisons of the cognitive abilities of cooperative and independent breeders need to be extended. Are the systematic cognitive effects of cooperative breeding observed in callitrichids also present in other taxa? If so, do they involve social cognitive abilities, nonsocial ones, or both?
- What is the exact link between prosociality and cooperative breeding? So far only a few species have been tested to provide evidence of this link, often using diverse experimental paradigms (see Box 1). A systematic assessment requires both reliable estimates of the extent of allomaternal care in different species[9,126] and a standardized paradigm for testing for prosociality across a wide range of species to provide truly comparable results.
- If there is a causal connection between prosociality and cognition, this should also be reflected in intraspecific variation, for example among individual capuchins or chimpanzees varying in prosociality, perhaps as a result of enculturation.
- The interpretation of the contrasts between humans and great apes with respect to division of labor, collective action, and life history would be strengthened if cooperative breeders in general differ from their independently breeding sister taxa in these characteristics.
- What dimensions of cooperative breeding are relevant to the questions we have posed? Cooperative breeding systems are far from uniform. They differ with regard to the degree of reproductive skew, the kind of helping performed by allomothers, the age-sex classes that serve as allomothers, and the relative stress levels of subordinates and dominants.
- The cooperative breeding hypothesis posits that alloparental care and provisioning provided the context for the evolution of many other derived features characterizing both human life histories and human sociocognitive and emotional traits. Consequently, the hypothesis predicts that life-history corollaries of cooperative breeding, such as longer childhoods, and behavioral corollaries, such as caring for disabled group members, should appear in the paleontological record at about the same time and early in the evolution of the line leading to *Homo sapiens*. Indeed, these corollaries should precede even more derived features such as fully sapient-sized brains, symbolic art, language, and cultural group selection. Although considerable debate persists about how to interpret the fossil record, there are certainly grounds to be optimistic about these predictions. [9,125,127]

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## ERRATUM

In Volume 16, Issue 5 (2007) of *Evolutionary Anthropology* "Evolutionary transformation of the hominin shoulder," by Susan G. Larson. Figure 7, displaying box and whisker plots of humeral torsion for comparative samples of apes, modern humans, and fossil, the torsion estimates for KNM-ER 739 and Omo 119-73-2718 had been inadvertently switched.