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REVIEW

Cognitive consequences of cooperative breeding in primates?

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Abstract Several hypotheses propose that cooperative breeding leads to increased cognitive performance, in both nonhuman and human primates, but systematic evidence for such a relationship is missing. A causal link might exist because motivational and cognitive processes necessary for the execution and coordination of helping behaviors could also favor cognitive performance in contexts not directly related to caregiving. In callitrichids, which among primates rely most strongly on cooperative breeding, these motivational and cognitive processes include attentional biases toward monitoring others, the ability to coordinate actions spatially and temporally, increased social tolerance, increased responsiveness to others' signals, and spontaneous prosociality. These processes are likely to enhance performance particularly in socio-cognitive contexts. Therefore, cooperatively breeding primates are expected to outperform their independently breeding sister taxa in socio-cognitive tasks. We evaluate this prediction by reviewing the literature and comparing cognitive performance in callitrichids with that of their sister taxa, i.e. squirrel monkeys, which are independent breeders, and capuchin monkeys, which show an intermediate breeding system. Consistent with our prediction, this review reveals that callitrichids systematically and significantly outperform their sister taxa in the socio-cognitive, but not in the non-social domain. This comparison is complemented with more qualitative evaluations of prosociality and cognitive performance in non-primate cooperative breeders, which suggest that among mammals, cooperative breeding generally produces conditions conducive to socio-cognitive performance. In the hominid lineage, however, the adoption of extensive allomaternal care presumably resulted in more pervasive cognitive consequences, because the motivational consequences of cooperative breeding was added to an ape-level cognitive system already capable of understanding simple mental states, which enabled the emergence of shared intentionality.

Keywords Cooperative breeding · Cognition · Callitrichids · Prosociality · Teaching · Shared intentionality · Cultural intelligence

Introduction

In the vast majority of mammal species, only the mother cares for the offspring until it becomes independent. In some species, however, individuals other than the mother assist in infant rearing (Macdonald 2001). This allomaternal care ranges from rather small contributions, such as when others occasionally allow infants to take relinquished food items, to reproductive systems in which an extensive amount of allomaternal care is offloaded to allomothers while mothers merely lactate (e.g., naked mole rats). Broadly defined, cooperative breeding refers to a reproductive system in which non-parent individuals help to care for and provision offspring (Wilson 1975; Ligon and Burt 2004). Snowdon (2001) suggested for non-human primates that cooperative breeding is linked to improved skills in socio-cognitive and communicative processes, and Hrdy (1999, 2005a, b, 2009), Burkart et al. (2009b), and van Schaik and Burkart (2009a) developed a similar argument for humans in the cooperative breeding hypothesis, by emphasizing the role of cooperative breeding in the emergence of uniquely human cognition.

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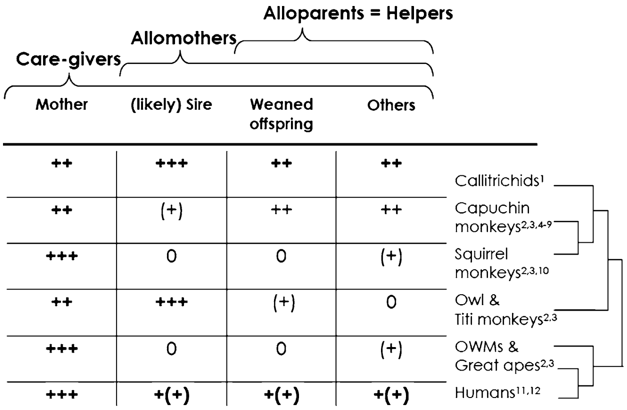
The aim of this review is to further explore the cognitive dimension of the cooperative breeding hypothesis, according to which extensive allomaternal care has a positive impact on cognition, by focusing on Callitrichidae, which among primates show the strongest reliance on cooperative breeding (Digby et al. 2007). We first develop expectations about which cognitive domains are most likely to be affected by cooperative breeding in primates, based on a list of tentative motivational and cognitive processes involved in the helping behaviors of callitrichids, extracted from their socioecology. We then evaluate these expectations by systematically reviewing the cognitive performance in different cognitive domains of callitrichids with those of their closest sister taxa, the independently breeding squirrel monkeys and the capuchin monkeys, which show an intermediate breeding system (Fig. 1). This is followed by a more qualitative evaluation of the hypothesis in other mammals that engage in extensive allomaternal care. Finally, we explore possible implications for our understanding of human cognitive evolution.

Allomaternal care and cooperative breeding in callitrichids

Allomaternal care is not rare among primates, but the strongest reliance on others in rearing young is present in the cooperatively breeding callitrichids (Hrdy 2009). They live in family groups typically composed of a breeding pair, its dependent offspring and helpers. Helpers are usually but not always the pair's offspring, and when mature, tend to be reproductively inactive (Digby et al. 2007). Rather than the mother, the main caregivers are often the father and older siblings, especially older brothers (Garber et al. 1984; König 1995; Kostan and Snowdon 2002). The caregivers carry the infants most of the time and provision them with food (Ferrari 1987; Feistner and Price 1990, 1991, 2000; Brown et al. 2004). Group members also cooperate in resource and territory defense and share vigilance duties (Koenig and Rothe 1991; Bales et al. 2000).



Mother	(likely) Sire	Weaned offspring	Others	
++	**+++**	**++**	**++**	Callitrichids[1]
++	(+)	++	++	Capuchin monkeys[2,3,4-9]
+++	0	0	(+)	Squirrel monkeys[2,3,10]
++	**+++**	(+)	0	Owl & Titi monkeys[2,3]
+++	0	0	(+)	OWMs & Great apes[2,3]
+++	**+(+)**	**+(+)**	**+(+)**	Humans[11,12]

Fig. 1 Extent of infant care by different classes of caregivers in selected primate taxa. Number of +'s indicate the intensity of caregiving but entries in *bold* refer to cases where caregiving includes more than occasional food sharing, grooming or playing with the infants (e.g. regular carrying, babysitting, active provisioning), whereas *parentheses* () indicate rare events or singular reports and 0 means the pattern is absent. *OWM* Old world monkeys. The *right-hand side* of the figure represents the phylogenetic relationship between these taxa according to Ray et al. (2005) and Steiper and Ruvolo (2003). [1]Digby et al. (2007), [2]Mitani and Watts (1997), [3]Ross and MacLarnon (2000), [4]Westergaard et al. (1999), [5]Fragaszy et al. (1997a, b), [6]O'Brien and Robinson (1991), [7]Perry (1996), [8]Fragaszy et al. (1991), [9]Baldovino and Bitetti (2008), [9]Fedigan et al. (2008), [10]Boinski and Fragaszy (1989), [11]Kramer (2005), [12]Sear and Mace (2008)

Socially, callitrichids are characterized by uniformly strong social bonds with virtually no aggression, and thus high social tolerance at the group level (Sutcliffe and Poole 1984; Digby 1994; Schaffner and Caine 2000; Aureli and Schaffner 2006). However, this general peacefulness can be punctuated by episodes of seriously escalated aggression, sometimes with lethal consequences when individuals compete for breeder status (Digby et al. 2007) or more rarely, group membership (Snowdon and Pickhard 1999). These periods are clearly demarcated, however, and usually do not involve all animals in the group.

Among independently breeding primates, food sharing with small immatures is rare and almost always passive. In callitrichids, in contrast, it is frequent and also includes active provisioning from any caregiver in the group to offspring. Active food sharing is initiated by the possessor who gives a food call, holds out the food item in its hand and waits for the immature to approach and take the food (reviewed in Brown et al. 2004). Indeed, the first solid food eaten by infant marmosets (*Callithrix jacchus*) is taken from the mouths and hands of carriers (Yamamoto 1993) rather than procured independently.

Why should cooperative breeding have cognitive consequences?

Extensive allomaternal care by multiple group members requires motivational and cognitive processes that might not be present in independent breeders, or only to a lesser degree. These processes, in turn, might lead to increased performance in cognitive tasks that are not directly linked to cooperative breeding per se.

A link between cooperative breeding and enhanced cognitive performance, in particular in the social domain, has been suggested from the perspective of adults in the case of callitrichids (Snowdon 2001; Rapaport 2006), and from the perspective of immatures in the case of humans (Chisholm 2003; Hrdy 2005a, 2009). We will now explore how this association might come about in some detail.

Motivational and cognitive processes involved in cooperative breeding

Caregivers

For caregivers, key behavioral elements of cooperative breeding include the coordination of activities such as vigilance, group and territory defense and care-giving (Fig. 2, upper part), the transfer of infants from one caregiver to the next, and food sharing/provisioning. The proximate regulation of these behavioral elements is based on motivational and cognitive processes (Fig. 2, middle part; C1–C4: cognitive processes, M1–M2: motivational processes), which in turn might translate in increased performance in a variety of cognitive tasks.

Consider coordination in infant carrying first. In the ancestral state, in which mothers alone carry infants, carrying infants is probably the result of the combination of high maternal motivation to be near and to carry infants and high responsiveness to subtle signals given by the infant whenever it needs to be carried. It is conceivable that infant carrying by helpers is achieved entirely by high responsiveness to infant signals. However, because helpers are not always in close proximity, this may lead to gaps in carrying or attendance that may be dangerous to the infants due to increased predation risk. Because increasing the intensity of distress calls merely increases the risk, such gaps are best avoided when alloparents are also continuously highly motivated to carry infants and therefore actively look for carrying opportunities. Observations show that infant transfers typically take place smoothly and infants are handed over directly from one caregiver to the next, and helpers are highly motivated (Zahed et al. 2007) and might even compete over infant carrying (Santos et al. 1997; Achenbach and Snowdon 1999; Schradin and Anzenberger 2003; Snowdon and Cronin 2007), indicating that they do so out of an intrinsic prosocial motivation.

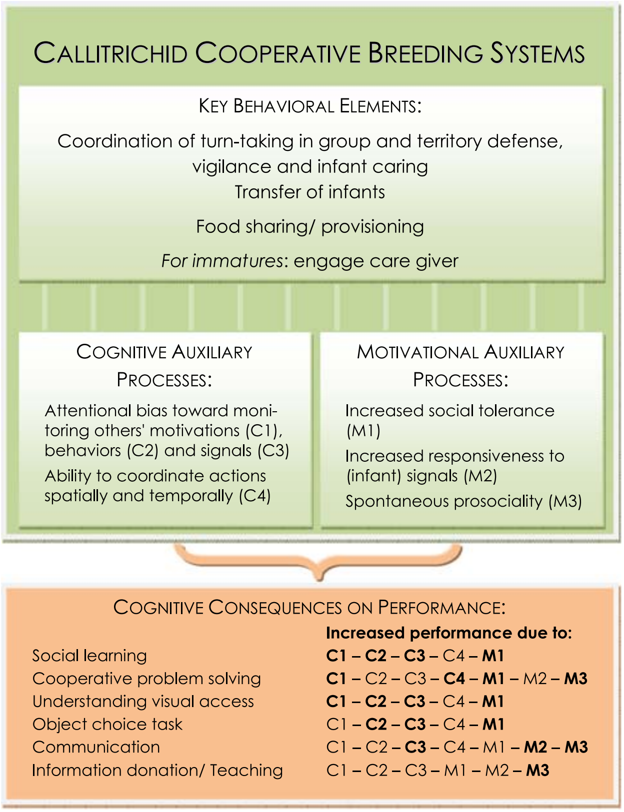


Fig. 2 Key behavioral elements (*upper part*) and motivational and cognitive processes (*middle part*) involved in cooperative breeding in primates. The *lower part* specifies how the presence of these motivational and cognitive auxiliary processes can also increase performance in a variety of socio-cognitive tasks. For example, performance in social learning tasks is strongly facilitated by the presence of the cognitive processes C1, C2 and C3 as well as the motivational process M3 (*bold*), and to a lesser extent (*not bold*) by C4

A second aspect of infant carrying is the coordination of the actual transfer of infants from one caregiver to the next. Effective infant transfer in the canopy requires high levels of social tolerance by alloparents, as well as the ability to coordinate behavior in space and time among alloparents, because failed attempts will result in infants falling to the forest floor, with its attendant risks (discussed in Schradin and Anzenberger 2003). This dyadic behavioral adjustment relies on carefully monitoring the behaviors and signals of the interaction partners. Snowdon and Boe (2003) point out that these propensities might be a factor explaining why, unlike other non-human primates, tamarins socially learn to avoid noxious foods by observing spontaneously occurring disgust reactions from conspecifics sampling the unpalatable food.

When it comes to provisioning by multiple helpers, responding to infants' begging alone might be insufficient, because infants will often be unaware that the helpers acquired the kind of food items usually shared, i.e. those that tend to be rare and difficult to obtain or process for infants (Price and Feistner 1993; Brown et al. 2004). Active provisioning may require that the motivation of an individual to offer especially nutritious food to infants is temporarily stronger than the motivation to eat it itself. Thus, helpers may need strong spontaneous provisioning motivations, because otherwise food would not be shared, let alone that calls be given to attract the infants. It might be argued that provisioning may also rely on the ability to inhibit the immediate impulse to eat the food by oneself and instead calling the infants and offer the food to them. However, if provisioning is regulated motivationally, increased inhibitory control is not mandatory because sharing becomes rewarding in itself.

This natural history of callitrichids suggests that at least some of their caregiving behaviors are regulated by spontaneous prosociality: a motivational predisposition to perform acts that benefit others, even in the absence of the expectation of reciprocation and solicitation by the recipient (e.g. begging, harassment). Importantly, 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 to actively impact others' circumstances in a positive way, a spontaneous helping impulse that does not have to be elicited through external signals such as 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 own benefits but also increases benefits to others (Fehr and Fischbacher 2003).

Experimental evidence indicates that unsolicited prosociality occurs in provisioning contexts in cooperatively breeding cotton-top tamarins (Hauser et al. 2003; Cronin and Snowdon 2008; but see Cronin et al. 2009) and common marmosets (Burkart et al. 2007), but not in independently breeding chimpanzees, not even in mother–infant dyads (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008), or in macaques (reviewed in Silk 2007). In capuchin monkeys, who show an intermediate breeding system (Fig. 1), modest levels of unsolicited provisioning have been reported (de Waal et al. 2008; Lakshminarayanan and Santos 2008), which appears consistent with the occurrence of active food sharing in this species, albeit at very low frequencies (de Waal 1997).

Two conclusions can be drawn. First, in most primate species, including chimpanzees, a general tendency toward spontaneous provisioning is absent, i.e. may at best occur in some special dyads and at low intensities, unlike in callitrichids and humans. This absence is evident under naturalistic conditions for all independently breeding primates and under experimental conditions in chimpanzees (see above). Thus, a high, generalized provisioning motivation may be limited to cooperative breeders.

Second, the cooperative behaviors in chimpanzees, in both the wild (Boesch 1994) and captivity (Warneken and Tomasello 2006; Warneken et al. 2007) may be regulated through mechanisms other than spontaneous prosociality. Instead, they may be the result of some form of expectation of reciprocation or a tendency to respond to requests (begging or harassment). Most importantly, the opposite is highly unlikely, i.e. that a species does not exhibit cooperative or prosocial behaviors, yet has prosocial motivational predispositions. For a more detailed discussion, see also Burkart et al. (2009b).

Care-recipients

Mothers in cooperative breeders tend to invest conditionally in their offspring, i.e. they might neglect or even abandon young if they perceive that insufficient allomaternal care is available (Hrdy 1999). As a result, infants of cooperative breeders should be under selection to engage caregivers, including their own mothers. This might even lead to the evolution of morphological features that are highly attractive to adults as well as increased behavioral solicitation of caregiving behaviors, reminiscent of the chase-away process of antagonistic sexual selection (Holland and Rice 1998). Hence, when emitting distress or begging vocalizations, immatures in cooperative breeders face different tradeoffs than immatures in independent breeders between indicating their need for help and the risk of attracting predators, and may therefore be less reluctant to advertise their neediness. The conspicuous and extensive babbling behavior of infant marmosets (Snowdon and Elowson 2001) might function as advertisement of their neediness.

The imminent risk of being abandoned might also favor the ability of immatures to discern (and maybe also manipulate) the motivations and intentions of potential alloparents. Hrdy (2005a) and Chisholm (2003) thus argue that from the perspective of the immatures, cooperative breeding provides an additional context in which the emergence of Macchiavellian social skills (Whiten and Byrne 1997) could be favored evolutionarily. However, this might apply to humans only, because (1) the cognitive abilities required might not be present in other cooperative breeders, and (2) in human societies, immatures are particularly likely to encounter individuals who do not qualify as potential alloparents or might even have hostile intentions toward them.

Impact on cognitive performance in non-caregiving contexts

The cognitive and motivational processes discussed in the previous section that are involved in the functioning of callitrichid cooperative breeding systems are also likely to influence cognitive performance in other contexts, as detailed in Fig. 2 (lower part). On the cognitive side, a pronounced attentional bias toward monitoring others (C1–C3 in Fig. 2) in relaxed contexts facilitates performance in most sociocognitive tasks, maybe particularly in social learning (including observational forms) and tasks assessing the understanding of gaze, e.g. object choice or perspective-taking tasks (see also Burkart 2009). It also sets the stage for more elaborate systems of communication through cooperative signaling (see also Snowdon 2001; Snowdon and Boe 2003), particularly in combination with an increased responsiveness towards other's signals (M2). Finally, it can be expected to increase performance in cooperation tasks, if accompanied by an ability to successfully coordinate actions with others in space and time (C4). This latter ability translates directly into increased performance in cooperative problem-solving tasks.

On the motivational side, social tolerance (M1) is well known to favor performance in many cognitive tasks that involve more than one individual, as first pointed out by Coussi-Korbel and Fragaszy (1995). Social tolerance permits individuals access to items that attract the interest of other group members who interact with those items (Russon 1997; van Schaik and Pradhan 2003; Whiten and van Schaik 2007). In addition, group-wide social tolerance can enhance sustained attention (Sarter et al. 2001) because individuals do not have to divide their attention between tasks and potentially aggressive dominant individuals.

Unsolicited prosociality (M3) may have cognitive consequences if it is general enough to also extend to contexts other than food, particularly to information or, in the case of humans, to mental states. An extension to information is suggested by the remarkable concentration of both provisioning and teaching (i.e. information donation) in cooperative breeders (see below), while an extension to mental states (i.e. shared intentionality) might be unique to humans, because other cooperative breeders presumably lack the ability to represent mental states per se (see below).

In sum, cooperative breeding can be expected to increase performance in the socio-cognitive domain, including social learning, communication, teaching-like behaviors, understanding of gaze and communicative cues as well as in cooperative problem solving. In non-social domains, however, such effects are less likely to arise directly. If they nonetheless occur, they suggest the operation of coevolutionary processes.

Cognitive correlates of cooperative breeding in nonhuman primates

A first indication suggesting that cooperative breeding has cognitive correlates stems from Snowdon's (2001) review. We extend his review in two ways. First, since 2001, more data on communicative and cognitive processes in callitrichids and other nonhuman primates have become available. Second, and more importantly, evaluating the cooperative breeding hypothesis in primates requires a systematic comparison of cognitive performance between the callitrichids and their more independently breeding phylogenetic sister taxa, which are the capuchin and the squirrel monkeys (Fig. 1). From current taxonomic work it is not clear whether the actual sister clade to the monophyletic callitrichids is the *Aotus* clade or the *Cebus–Saimiri* clade (e.g. Canavez et al. 1999; Steiper and Ruvolo 2003; Ray et al. 2005; Bininda-Emonds et al. 2007), probably because the three lineages diverged at a very similar time. We chose the *cebine* clade (*Cebus–Saimiri*) for comparison because the extensive male care in *Aotus*, occasionally even accompanied by helping by immatures (Jantschke et al. 1998), makes it more difficult to identify clear contrasts.

Members of the *Cebus–Saimiri* clade are largely independent breeders (Jack 2007, Fig. 1). In squirrel monkeys (*Saimiri spp*), infants spend little time with, and have little opportunity to monitor, foraging adults at close proximity, even including their own mothers (Boinski and Fragaszy 1989). Group members are not universally attracted to offspring and might even respond to their presence with a rise in cortisol (Soltis et al. 2003). In capuchin monkeys (*Cebus spp*), some allomaternal investment in the form of allomaternal carrying and suckling of older infants between the ages of 3 and 6 months and low levels of allomaternal provisioning is present (O'Brien and Robinson 1991; Fragaszy et al. 1991, 1997a; Perry 1996; Brown et al. 2004; Baldovino and Bitetti 2008; Fedigan et al. 2008) but food sharing is rare and generally follows a reciprocal pattern (Westergaard et al. 1999).

The approach of directly comparing callitrichids to the *Saimiri*/*Cebus* clade provides a conservative test of the hypothesis that extensive allomaternal care enhances cognitive performance because of the smaller brain size of callitrichids compared to their sister taxa (most callitrichid brain sizes are ca. 4 times smaller than *Saimiri* and ca. 6 times smaller than *Cebus*, Herculano-Houzel et al. 2007), and the association between brain size and cognitive performance (Deaner et al. 2007; Reader and Laland 2002) for which we cannot control in this comparison. Hence, everything else being equal, one would expect that callitrichids have far less elaborate cognitive abilities than their sister groups.

Whenever comparable data of a given cognitive task with information for callitrichids was missing for their sister groups, we used data from the next closest platyrhine or cercopithecine taxa for which data was available. This approach is even more conservative because these taxa typically possess even bigger brains. We only included studies that were sufficiently comparable with regard to settings and methodology employed. Nevertheless, it is well known that even subtle differences in the settings sometimes affect outcomes considerably (e.g. Karin-D'Arcy and Povinelli 2002; Bräuer et al. 2007), for which we cannot account in this review. However, there is no reason to assume such effects would consistently favor one taxon over the other, and consistent differences are therefore likely to be real. The comparison of cognitive performance of callitrichids and their phylogenetic sister taxa, for both the social and the non-social domains, are summarized in Tables 1 and 2.

Comparison of cognitive performance in the social domain

Social learning

An overview of all social learning studies in primates published between 1950 and 2002, both from the wild and from

Table 1 Comparison of socio-cognitive performance between cooperatively breeding primates (Callitrichidae) and their independently breeding sister taxa (*Cebus* and *Saimiri*)

	Callitrichids		Sister taxa	Which taxa?
Social learning				
Percentage of successful social learning studies since 1950 (Custance et al. 2002)	100%	>	43%	*Cebids*
Social facilitation of acceptance of novel foods by infants	Vitale and Queyras (1997), Yamamoto and Lopes (2004), Voelkl et al. (2006), Rapaport (1999)	>	Fragaszy et al. (1997b)	*Cebus apella*
Begging for information	Voelkl et al. (2006), Rapaport (1999)	>	Fragaszy et al. (1997b), Boinski and Fragaszy (1989)	*Cebus apella, Saimiri oerstedi*
Learning food aversions	Snowdon and Boe (2003)	>	Visalberghi (1994), Visalberghi and Addessi (2000a)	*Cebus apella*
Imitation in two-action tasks (copy the topography of an action)	Bugnyar and Huber (1997), Voelkl and Huber (2000, 2007), Caldwell and Whiten (2004)	=	Price and Caldwell (2007), Custance et al. (1999), Fredman and Whiten (2008)	*Colobus guereza kikuyuensis*; *Cebus apella* (enculturated)
Social learning through scrounging	Caldwell and Whiten (2003)	>	Fragaszy and Visalberghi (1989)	*Cebus apella*
Vocal communication				
Vocal contextual learning	Pistorio et al. (2006), Roush and Snowdown (2001)	=	Hauser (1989), Seyfarth and Cheney (1986)	*Cercopithecus aethiops*
Vocal production learning				
Acquisition of call repertoire	Snowdon (2001), Elowson et al. (1992, 1998a, b), Snowdon and Elowson (2001)	>	Winter et al. (1973), Hammerschmidt et al. (2001), Egnor and Hauser (2004)	*Samiri sciureus*
Plasticity of vocal signals in adulthood	Schrader and Todt (1993), Norcross and Newman (1993), Snowdon and Elowson (1999), Elowson and Snowdon (1994), Rukstalis et al. (2003), De la Torre and Snowdon (2002), Weiss et al. (2001)	≥	Lieblich et al. (1980), Newman and Symmes (1982), see also Egnor and Hauser (2004)	*Saimiri sciureus*; but mouse lemurs, three macaque species and chimpanzees
Teaching-like behaviors				
In the wild	Rapaport and Ruiz-Miranda (2002)	>	e.g. Boesch (1991), Boinski and Fragaszy (1989), Lonsdorf (2006)	*Saimiri oerstedii*, Chimpanzees
In captivity	Roush and Snowdown (2001), Humle and Snowdon (2008), Dell'Mour et al. (2009)	>	Fragaszy et al. (1997a)	*Cebus apella*
Gaze understanding				
Object choice tasks	Neiworth et al. (2002), Burkart and Heschl (2006)	>	Itakura and Anderson (1996), Vick and Anderson (2000)	*Cebus apella*
Sensitivity to the predictive value of gaze	Santos and Hauser (1999)	>	Anderson et al. (2004)	*Saimiri sciureus*, *Cebus apella*
"Perspective taking"	Burkart and Heschl (2007)	>	Hare et al. (2003)	*Cebus apella*
Cooperation				
Occurrence across age and sex classes in the wild	Digby et al. (2007)	>	Rose (1997), Boinski (1994), Boesch (1994, 2002), Mitani et al. (2002)	*Cebus capuchinus*, *Saimiri oerstedii*, *chimpanzees*
Cooperative problem solving	Werdenich and Huber (2002), Cronin et al. (2005), Snowdon and Cronin (2007), Cronin and Snowdon (2008)	≥	Reviewed in Snowdon and Cronin (2007)	*Cebus apella*, chimpanzees, orangutans

If no information is available for one of the immediate sister taxa, the next closest primate taxon is used. ">" indicates stronger performance in callitrichids, "<" lower and "=" comparable performance

Table 2 Comparison of cognitive performance between cooperatively breeding primates (Callitrichidae) and their independently breeding sister taxa (*Cebus* and *Saimiri*) in physical and other non-social domains

	Callitrichids		Sister taxa	Which taxa?
General cognitive ability (Deaner et al. 2006), derived from learning sets, patterned-string problems, reversal learning, delayed response, invisible displacement	−1.22	<	Capuchins: +0.19 Saimiri: −0.94	*Capuchins*, *Saimiri*
Object permanence stage VI	Stage VI (Neiworth et al. 2003; Mendes and Huber 2004)	> ≥	De Blois et al. (1998) Schino et al. (1990)	*Saimiri sciureus* *Cebus apella*
Working memory of action (at delays of 1, 2, 4 and 8 s, Tsujimoto and Sawaguchi 2002)	0.53, 0.33, 0.2, 0.18	<	0.63, 0.64, 0.41, 0.18	*Saimiri sciureus*
Innovation rates (from Lefebvre et al. 2004)	−1.7	<	−0.75 (A), −0.4 (B)	A = *S. sciureus* B = *C. albifrons*
Tool-use rates (from Lefebvre et al. 2004)	−1.6	<	−1.4 (A), 0.4 (B)	A = *S. sciureus* B = *C. albifrons*
Patience	Stevens et al. (2005)	< <	Rosati et al. (2007), Addessi et al. unpublished	Chimpanzees *Cebus apella*
Inhibitory control (reverse contingency task)	Kralik et al. (2002)	=	Anderson et al. (2000)	*Saimiri sciureus*
Food quantity discrimination	Stevens et al. (2007), Exp 1	<	Addessi et al. (2008), Exp 1	*Cebus apella*

If no information is available for one of the immediate sister taxa, the next closest primate taxon is used. ">" indicates stronger performance in callitrichids, "<" lower and "=" comparable performance. The numbers in second and fifth columns represent directly comparable quantifications of performance, with higher values indicating higher performance

captivity was collated by Custance et al. (2002). While in callitrichids, all collected data sets (5/5) provided evidence for social learning, positive effects were detected in only 43% (10/23) in cebines ($X^2 = 26.4$, $P < 0.001$). This supports the prediction that callitrichids perform particularly well in social learning.

The *acceptance of novel foods by infants* is socially facilitated in callitrichids. Thus, common marmoset twins tested together either refused or ate only small amounts of novel foods in the absence of adults (Voelkl et al. 2006). Instead, they accepted novel foods more readily if they could observe that adults were eating the same food (Vitale and Queyras 1997; Yamamoto and Lopes 2004; Voelkl et al. 2006). Similarly, infants of both golden lion tamarins and common marmosets were more likely to eat novel food items received from adults than those that they had acquired independently (Rapaport 1999; Voelkl et al. 2006). No such social facilitation was apparent in capuchin infants (Fragaszy et al. 1997b), who ate novel foods as readily when these were presented away from adults as when presented to the whole group. This difference may arise because callitrichid infants appear to optimize learning about novel foods by actively seeking to obtain food items unknown to them from more experienced adults rather than getting these items independently (Voelkl et al. 2006), whereas infant capuchins (Fragaszy et al. 1997b) and squirrel monkeys (Boinski and Fragaszy 1989) are not actively looking for information from adults.[1]

Using social information to *learn food aversions* is rare among primates and the few informal observations are not supported by formal evidence (reviewed in Visalberghi

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[1] Whether social influences on the acceptance of novel foods by *adults* (Visalberghi and Addessi 2000a, b, 2003; Addessi et al. 2007) also differ between callitrichids and their sister taxa cannot be decided conclusively on the basis of the data currently available. Addessi et al. (2007) found that in two species of cooperatively breeding primates, in marmosets (*Callithrix jacchus*) and in Goeldi's monkeys (*Callimico goeldii*), the acceptance of novel food was not increased by group mates eating either the same or different food, as compared to the mere presence of group mates not eating anything. In the same study, Goeldi's monkeys, but not marmosets, paid more visual attention if their group mates were eating the same novel food. However, different results might have been obtained if novelty levels had been adjusted more closely to species-typical affordances because the neophobic Goeldi's monkeys never tasted the new food in any condition, whereas common marmosets' responsiveness was very high already in the presence condition, presumably resulting in a ceiling effect in the other conditions. Capuchin monkeys were tested in a similar setting (Visalberghi and Addessi 2000b), and the kind of food the group mates were consuming also did not affect the acceptance of novel foods. However, no comparison of the social influence alone is possible because the callitrichids, unlike the capuchins, were not tested in a control condition with novel food in the absence of group members. In addition, there is evidence that experimentally induced food aversions can be reversed through interaction with non-averse conspecifics in adult common marmosets (Queyras et al. 2000) and tamarins (*Saguinus fuscicollis* and *Saguinus labiatus*, Prescott et al. 2005), but comparative data from sister taxa are again lacking.

1994). For instance, capuchins did not rely on the reactions of conspecifics towards food items that had been made unpalatable by experimenters, but their behavior suggests that each individual, infants included, discovered the food palatability on its own (Visalberghi and Addessi 2000a). However, experimental evidence suggests that tamarins (*Saguinus oedipus*) can learn socially to avoid a preferred food when it was made unpalatable (Snowdon and Boe 2003). For squirrel monkeys (*Saimiri oerstedi*), a single field observation seems to suggest social transmission of selective avoidance of hazardous caterpillars (Boinski and Fragaszy 1989). However, given that the same publication reported virtually no opportunities for social learning in the feeding context, it is likely that this anecdote has to be interpreted in the context of avoidance of predators and danger rather than food aversion. In contrast to food aversions, predator avoidance is easily acquired socially in many nonhuman primates (Mineka and Cook 1988; Cheney and Seyfarth 1990; Heyes 1994). Hence, the social learning of food aversions seems to be present in tamarins, but not in capuchin and squirrel monkeys.

Observational forms of social learning, such as *imitation*, are not widespread in non-human primates, and their presence has been questioned for years even in great apes (Tomasello 1996; Dautenhahn and Nehaniv 2002; Whiten et al. 2004). Although many taxonomies and definitions of the various forms of social learning exist (e.g. Whiten and Ham 1992; Caldwell and Whiten 2002; Call and Carpenter 2002; Whiten et al. 2004), there is consensus that observational forms of social learning that result in the copying of behavior are cognitively more complex and that they can be classified according to which aspects of the behaviors are copied, e.g. their goal, their result, or their topography. The only monkey species in which, using a two-action method, copying of the exact topography of an action was found was the common marmoset (Voelkl and Huber 2000, 2007). Other results of social learning tasks with common marmosets (Bugnyar and Huber 1997; Caldwell and Whiten 2004; Humle and Snowdon 2008; Burkart et al. 2009a) allow less precise identification of the specific mechanisms involved, but are all at least consistent with this finding.

Human-reared capuchin monkeys from a helping-hands project showed instances of social learning in an artificial fruit task that clearly went beyond stimulus enhancement (Custance et al. 1999), and also copied actions demonstrated by humans in a two-action tasks (Fredman and Whiten 2008). However, action copying was not found in a mother-reared control group, suggesting an enculturation effect similar to the one observed in apes (reviewed in van Schaik and Burkart 2009b). Since zoo-living groups of colobus monkeys did socially learn from a conspecific a simple push-or-pull technique to open a door (Price and Caldwell 2007), the ability to copy simple actions might not be unique to callitrichids. In sum, evidence that common marmosets' imitation performance exceeds that of capuchin monkeys is not entirely compelling, but their performance is at least as good.

Finally, adult common marmosets and capuchin monkeys differ with regard to the effect that the opportunity for *scrounging* from a skilled conspecific has on social learning. While the opportunity for scrounging is generally thought to inhibit social learning and indeed did so in capuchin monkeys (Fragaszy and Visalberghi 1989), the opposite effect was found in common marmosets whose social learning increased if they had the opportunity to scrounge (Caldwell and Whiten 2003). The difference in the effect of scrounging is consistent with the greater tendency toward social learning in callitrichids. It is important to note, however, that social learning in callithrichids does not necessarily involve scrounging and can indeed occur very rapidly (Moscovice and Snowdon 2006).

Vocal communication

The flexibility and complexity of a communication system can be increased if it can be subjected to experiential influences. Janik and Slater (2000) distinguish between two categories of vocal learning: contextual learning (i.e. learning about the behavioral context or serial position of a signal) and vocal production learning (i.e. the modification of a vocal signal). *Vocal contextual learning* is present in various primates (cf. Seyfarth and Cheney 1986; Fichtel 2008) and also in marmoset infants who use many call types in the absence of context and only later use them in appropriate ways (Pistorio et al. 2006), and has been demonstrated in detail for cotton-top tamarin chirp vocalizations (Roush and Snowdown 2001). Unfortunately, no data are available for capuchin and squirrel monkeys.

In spite of being widespread in many bird species, *vocal production learning* in mammals is rare and mainly restricted to humans, bats, whales, dolphins and elephants (Egnor and Hauser 2004; Webb and Zhang 2005; Poole et al. 2005). Accordingly, isolation-reared squirrel monkeys produce all call types of the species-specific vocal repertoire (Winter et al. 1973; see also Hammerschmidt et al. 2001). In contrast, there is some indication that social influences play a role in the acquisition of the adult repertoire in marmosets (Snowdon 2001). For example, the pattern of developmental change in pygmy marmoset trill vocalizations is not consistent with the one expected due to physical maturation alone (Elowson et al. 1992).

Unlike any other non-human primate studied to date, infant pygmy marmosets engage in babbling behavior, similar to babbling in human infants (Elowson et al. 1998a, b). Because social interactions between adults and infants are increased during babbling, and the amount and diversity of babbling is related to the quality of vocal production at the end of infancy (Snowdon and Elowson 2001), babbling may facilitate vocal learning.

Flexible accommodation of vocalizations in response to social changes, indicating the ability to alter vocal structure well into adulthood, represents another instance of vocal production learning in callitrichids. Common marmosets placed in isolation from their group mates modify the acoustic structure of their phee call (Norcross and Newman 1993; Schrader and Todt 1993). More tellingly, newly paired pygmy marmosets tend to converge on a common structure in their "trill" calls (Snowdon and Elowson 1999) and the introduction of new animals resulted in changed call structures in all age classes of captive pygmy marmosets (Elowson and Snowdon 1994) and Wied's black tufted-ear marmosets (Rukstalis et al. 2003). Furthermore, different populations may display systematic differences in call structure (Weiss et al. 2001; De la Torre and Snowdon 2002). These results suggest "a degree of plasticity in vocal signals that is rare among non-human primates" (Rukstalis et al. 2003). Such plasticity of vocal signals in adulthood has not been found in squirrel monkeys (Lieblich et al. 1980; Newman and Symmes 1982), strongly suggesting that vocal plasticity is greater among callitrichids than its cebine sister group. However, vocal plasticity among adults might be less rare among non-human primates than previously thought, having been demonstrated for mouse lemurs, three macaque species and chimpanzees (reviewed in Egnor and Hauser 2004).

Teaching

Typical social learning situations in non-human primates do not include an active role for the knowledgeable individual, and teaching is also rare in other non-human animals (Leadbeater et al. 2006; Csibra 2007). Operationally, a behavior qualifies as teaching if it only occurs in the presence of a naïve observer, is not immediately beneficial to the potential teacher but implies some costs, and if the observer profits from this behavior in terms of facilitated knowledge acquisition or skill learning (Caro and Hauser 1992).

The most suggestive evidence supportive of teaching among non-human primates has been found in callitrichids (Rapaport and Ruiz-Miranda 2002, 2006; Rapaport 2006; Dell'Mour et al. 2009). Rapaport and Ruiz-Miranda (2002) report three observations from two different groups of wild golden lion tamarins (*Leontopithecus rosalia*) that satisfy the criteria for tutoring by Caro and Hauser (1992). Roush and Snowdon (2001) experimentally demonstrated that food transfers accompanied by vocalizations provide an opportunity for infants to learn both about the foods and the appropriate vocalizations, which therefore could represent a form of coaching (i.e. the encouragement or discouragement of infants' behaviors; Caro and Hauser 1992) or information donation. Begging success of tamarins in the wild depends on whether the alloparent vocalizes a particularly rapid and intensified version of adult food calls (Joyce and Snowdon 2007), thus enabling selective withdrawal of food transfers as infants acquire independent feeding, which may represent a form of scaffolding. Accordingly, Humle and Snowdon (2008) found instances of behavioral scaffolding of infant problem-solving attempts by parents in an experiment with cotton-top tamarins. In contrast, reports of behaviors that might qualify as teaching in other non-human primates are very scarce (e.g. Boinski and Fragaszy 1989; Boesch 1991) and attempts to systematize and quantify corresponding observations typically fail (e.g. Lonsdorf 2006), indicating that teaching in other non-human primates, including chimpanzees, is rare at best (Matsuzawa et al. 2001).

Teaching can be construed on a continuum from being a narrow adaptation to a complex skill depending on mental state attribution in the form of the appreciation of the knowledge state of another individual, implying that the teacher has to be responsive to the fact that her own and the learner's knowledge state differ (e.g. Baron-Cohen 1999; Cheney and Seyfarth 2007; Premack 2007). At one end, teaching evolves as a simple behavioral program triggered under specific conditions and is of limited content. Therefore, it is expected to only occur in a narrow, predefined range of situations and problems and not to be applied flexibly under novel circumstances. In addition, the information about the knowledge state of the learner, which is necessary to meet the criterion that the learner has to be naïve (Caro and Hauser 1992), must be implemented in the specific conditions that trigger the teaching behavior rather than represented internally by the teacher. For example, a simple heuristic to meet the naïve observer criterion is that teaching is automatically applied toward youngsters of a specific age range who are therefore most unlikely to have gained critical experience or acquired the relevant skill. In this case, the prediction is that age, rather than the naïve individual's skill or knowledge state are critical for the occurrence of teaching behavior by adults. This seems to be the case in many carnivores that bring back (live) prey to their offspring (Caro and Hauser 1992; Thornton and McAuliffe 2006).

Where on the continuum between simple adaptations and human-like mentalistic forms of teaching can we locate callitrichids? With regard to content, all known instances of teaching are related to foraging. Nevertheless, cotton-top tamarins showed scaffolding behaviors in a complex, artificial foraging task never encountered before (Humle and Snowdon 2008), indicating at least some flexibility.

With regard to the naïve observer criterion, the critical question is how callitrichids can produce teaching behaviors that are sensitive to the knowledge state of their offspring. There are several indications that age alone is not decisive. In food-sharing interactions, adults discriminate between foods that are known to infants and foods that are novel to them, in lion tamarins (Price and Feistner 1993; Rapaport 1999), common marmosets (Vitale and Queyras 1997; Brown et al. 2005 but see Voelkl et al. 2006) and cotton-top tamarins (Feistner and Price 1990), even though variation in the direction of these effects is not fully understood (Voelkl et al. 2006). Moreover, in a longitudinal study, cotton-top tamarin parents discriminated between infants who were able and were not able to solve a foraging task and were reluctant to share with infants who could handle the apparatus by themselves, independent of the age of the infants (Humle and Snowdon 2008). In contrast, adult capuchins' tolerance did not differ between infants that could open nuts by themselves or that could not (Fragaszy et al. 1997a), even though details of the two studies differ.

In sum, among non-human primates, the most persuasive evidence for teaching is found in callitrichids, and there is evidence that these behaviors go beyond narrow adaptations triggered under specific conditions. However, the limitations of the flexibility of these behaviors still have to be delineated.

Understanding of gaze and communicative cues

Non-human primates typically have difficulty in using gaze or other communicative cues such as touching or pointing to localize hidden objects (reviewed in Call et al. 2000; Emery 2000; Burkart and Heschl 2006). Capuchin monkeys were able to use point but not gaze cues (head and eye movements, Anderson et al. 1995), even though they learned to use gaze cues after extensive training (Itakura and Anderson 1996; Vick and Anderson 2000). Common marmosets successfully used tap-, point- and gaze-cues, including eyes-only cues in a modified, and therefore not directly comparable setting (Burkart and Heschl 2006). Nevertheless, they proved to be very accurate in exactly determining the specific target of the gaze, and cotton-top tamarins performed particularly well with tap-, point- and gaze cues, even in the absence of training (Neiworth et al. 2002). Sensitivity to the predictive value of gaze on subsequent actions was found in cotton-top tamarins, based on an expectancy-violation paradigm (Santos and Hauser 1999). In contrast, squirrel monkeys and capuchin monkeys did not use another's gaze to predict its future actions (Anderson et al. 2004).

Of particular interest is whether non-human primates are able to construe gaze as a mental event, i.e. if they understand that other individuals can visually perceive the world as they do themselves. The simplest form of mentalistic gaze understanding refers to whether individuals discriminate between what others can or cannot see (i.e. level-1 perspective taking, Flavell 1985). Such an understanding has been demonstrated for chimpanzees using a competition task in which a subordinate individual had the choice between a piece of food that was freely visible to a dominant competitor and a piece of food that was hidden from its view (Hare et al. 2000). When forced through a small headstart to make an active choice, subordinate chimpanzees preferably retrieved the piece of food invisible to the dominant. While subordinate capuchin monkeys failed in this task (Hare et al. 2003), subordinate common marmosets showed the same preference for the hidden piece of food as chimpanzees (Burkart and Heschl 2007). Subsequent experiments revealed that the marmosets probably relied on a different mechanism than level-1 perspective taking, i.e. that they perceived the conspecific's gaze as indicating a possessive relationship between looker and target object. Nonetheless, the marmosets outperformed the capuchin monkeys in this task (Burkart 2009).

Cooperation and cooperative problem solving

Among wild primates, cooperative behaviors are most widespread in callitrichids (Campbell et al. 2007), where they occur in all age and sex classes (except infants: Digby et al. 2007). Because naturalistic observations rarely permit recognition of the mechanisms involved in cooperative interactions, experimental approaches were used.

Common marmosets are able to coordinate their behaviors in space and time in order to solve a problem cooperatively (Werdenich and Huber 2002). The same was found in cotton-top tamarins in a task that required simultaneous extension of two handles that were too far apart for a single tamarin to access both (Cronin et al. 2005). The tamarins solved 97% of trials and showed some understanding of the role of the partner, as reflected in reduced pulling rates when the partner was absent. Capuchin monkeys also coordinate their behavior in space and time in a cooperative barpull task (Brosnan et al. 2006), but Snowdon and Cronin (2007) emphasized that the efficiency of tamarins appears to be higher than in both capuchins and chimpanzees. Furthermore, the tamarin cooperation also continued when only one individual received rewards (Cronin and Snowdon 2008). Thus, cooperation is more common and possibly better coordinated in callitrichids than in cebines, both in the wild and in captivity.

Comparison of cognitive performance in the non-social domain

In a recent meta-analysis, Deaner et al. (2006) compared the performance of different primate taxa in non-social cognitive tasks, including detour problems, patterned-string problems, invisible displacement, tool use, object discrimination learning sets, reversal learning, oddity learning, sorting, and delayed response. The results of this meta-analysis revealed that performance on these different tasks is strongly correlated across different genera and that the overall performance can be described using a single, global variable. On this variable, the genus *Callithrix* is outperformed by both *Saimiri* and *Cebus* (Table 2), indicating lower general cognitive ability in the non-social domain in *Callithrix* as compared to its sister taxa.

The inclusion of studies not included in the meta-analysis of Deaner et al. (2006) does not change this conclusion. For example, Tsujimoto and Sawaguchi (2002) report higher performance levels in working memory of action in *Saimiri sciureus* than in *C. jacchus*, and both tamarins and marmosets were far outperformed by chimpanzees (Rosati et al. 2007) and capuchin monkeys (Addessi et al. unpublished) in a task requiring them to forgo an immediate benefit in order to obtain a larger benefit later on. In a comprehensive compilation of data from different sources, Lefebvre et al. (2004) found higher innovation and also tool use rates in both *Cebus apella* and *S. sciureus* than in *C. jacchus*. On the other hand, two invisible displacement studies, in common marmosets (Mendes and Huber 2004) and cotton-top tamarins (Neiworth et al. 2003), demonstrate stage VI object permanence, which has not been found in squirrel monkeys (de Blois et al. 1998) and not consistently in cebus monkeys (Schino et al. 1990; Dumas and Brunet 1994).

Data allowing a comparison of inhibitory control come from reversed contingency tasks, in which subjects have to reach for a smaller amount of food in order to receive a bigger amount (and therefore have to inhibit the pre-potent action tendency to reach for the bigger amount of food). All non-human primates show major difficulties in solving this task (reviewed in Genty et al. 2004), and due to methodological differences it is not possible to date to identify whether cotton-top tamarins (Kralik et al. 2002) and squirrel monkeys (Anderson et al. 2000) perform differently.

Conclusions

Future evaluations of the performance of callitrichids on non-social tasks should use more quantitative approaches that explicitly control for the effect of brain size. In the socio-cognitive comparisons this was not necessary because the smaller-brained callitrichids outperformed their larger-brained sister taxa. One promising avenue is to relate performance in specific tasks, e.g. reversal learning (Gaudio and Snowdon 2008) to brain size across species, and then examine the residual performance.

Our prediction was that callitrichids would outperform their sister taxa in the social, but not necessarily in the non-social domain. Overall, we identified 12 social subdomains and 7 non-social subdomains for which sufficiently comparable data are available (see Tables 1, 2). Consistent with our expectation, callitrichids performed better in all social subdomains, and worse in all but one of the non-social subdomains ($X^2 = 14.3$, $P < 0.001$).

Cognitive correlates of cooperative breeding in non-primates

Each breeding system based on extensive allomaternal care by multiple group members can be characterized by key behaviors performed by the members of the group. Accordingly, the motivational and cognitive processes regulating these behaviors are expected to vary depending on the details of the system. For instance, in some lineages, helping may consist largely of provisioning whereas in others coordinated vigilance or infant carrying is the prime activity of helpers. Still, the same basic prosociality may characterize all cooperative breeders, even if details of the caregiving behaviors vary. Here, as a preliminary evaluation of the possibility that cooperative breeding, prosociality and increased socio-cognitive performance are also linked in non-primates, we survey the literature on other cooperative breeders.

Prosociality

The natural history of canids, many of whom are cooperative breeders (Macdonald and Sillero-Zubiri 2004a), suggests a prosocial psychology. Alloparental care in African wild dogs (*Lycaon pictus*) includes babysitting (chasing away predators, ensuring that pups do not stray and returning them to the den in case of danger) and provisioning upon return from a hunt (Malcolm and Marten 1982) by regurgitation or, less often, by carrying portions of a carcass to the den (Creel and Creel 2002). Groups rear pups even if the mother dies and may also adopt unrelated pups (Estes and Goddard 1967; McNutt 1996), suggesting that allomaternal investment is not limited to closely related pups or the result of coercion by the dominant female but regulated by intrinsic motivational forces. Adoption has also been recorded in red foxes, *Vulpes vulpes* (Macdonald 1979). Furthermore, canids provision pregnant and lactating mothers, or other individuals, usually females, who stay at the den with the pups while the rest of the pack hunts (Macdonald and Sillero-Zubiri 2004b). Older pups who already move with the pack are often left behind during hunts and later recovered (Creel and Creel 2002). They are either accompanied by adult babysitters of either sex, or, if left alone, retrieved by any pack member and led to the kill. Pups are allowed to feed first, followed by yearlings and then adults. Both African wild dogs and red foxes even care for injured group members. In wild dogs, incapacitated and older pack members are tolerated at kills (Estes and Goddard 1967), and adult red foxes might actively feed injured adult group members (Macdonald 1987), indicating that the helping impulse extends to other group members than immatures, similar as in callitrichids. In conclusion, despite a lack of experimental evidence, the behavior of African wild dogs and red foxes strongly suggest the presence of a motivational predisposition toward spontaneous prosociality (i.e. a helping impulse) similar to the one found in the cooperatively breeding primates (marmosets and humans).

Another mammal engaging in extensive allomaternal care are elephants. In particular reproductively inactive females engage in extensive allomothering, which plays a vital role in calf growth and survival (Lee and Moss 1986; Poole and Moss 2009). Similar to callitrichids and canids, they show many cooperative behaviors in the wild, e.g. in predator deterrence or the acquisition of food or water, but also in the form of regular targeted helping, such as physically supporting weak animals in climbing up a slope (Schulte 2000) and assisting injured or disabled group members (Hart et al. 2008). Cooperative behaviors, including allomaternal care, are not restricted to related individuals and can take very strong forms as in the case of a dominant female who adopted the calf of an unrelated, subordinate group member (reviewed in Bruce 2000; Poole and Moss 2009). Thus, elephants may also exhibit spontaneous prosociality, although again experiments are lacking to date.

Cognition

As to evidence for cognitive abilities in these non-primates, the record is perhaps most impressive for canids (reviewed in Udell and Wynne 2008). Recent experiments revealed socio-cognitive performance in dogs that seriously rival ape performance, for example:

- understanding of visual perspective and mental states (Bräuer et al. 2004; Viranyi et al. 2004; Topal et al. 2006)
- victim-directed third-party post-conflict affiliation, i.e. “consolation” (Cools et al. 2008)
- reasoning by exclusion in a social context (Kaminski et al. 2004)
- sophisticated passive (use of experimenter-given cues) and active communicative abilities (Miklósi et al. 1998, 2000)
- cooperation skills (Naderi et al. 2001)
- imitation (Topál et al. 2006), including selective inferential imitation (Range et al. 2007).

In the non-social and physical realm, dogs perform less impressively (e.g. Osthaus et al. 2003; Bräuer et al. 2006; Dumas and Pagé 2006; Udell et al. 2008b but see Ward and Smuts 2007), even though such studies are rarer and therefore more difficult to evaluate. Nevertheless, dogs seem to outperform e.g. cats in at least some tasks (Doré et al. 1996), and in some cases, their non-social cognitive abilities might be overruled by social problem-solving strategies (Erdohegyi et al. 2007).

In canids, these socio-cognitive abilities have been attributed to domestication effects (e.g. Hare et al. 2002; Miklosi and Csanyi 2004; Hare and Tomasello 2005; Topal et al. 2005), and empirical data generally support this view (e.g. Hare et al. 2005; Topal et al. 2005, but see Wynne et al. 2008; Udell et al. 2008a). The domestication hypothesis, however, cannot explain that despite very long histories of domestication, comparable effects did not arise in any of the numerous other species that were domesticated. Moreover, experimentally induced domestication in foxes (Trut 1999) produced similar enhancements in socio-cognitive performance, and did so much faster than in the domestication history of cats (Hare et al. 2005). Foxes, like wolves, show extensive alloparental care by multiple group members (Macdonald 1979; Baker and Harris 2004). Thus, this pattern of results suggests the socio-cognitive consequences of the domestication of dogs arose because the wolf ancestor already had specific socio-cognitive adaptations to cooperative breeding (Virányi et al. 2008; Udell et al. 2008a), which could be further promoted and directed at humans through selective domestication.

Likewise, the socio-cognitive performance of elephants repeats the pattern of callitrichids: with the exception of their memory capacity, in many non-social cognitive tasks their performance is unimpressive given their large brains, but they excel in socio-cognitive tasks (reviewed in Hart et al. 2008), e.g. mirror self-recognition or vocal imitation (Poole et al. 2005).

Discussion

Cooperative breeding and cognition

In agreement with the cooperative breeding hypothesis, the performance of callitrichids in socio-cognitive contexts generally exceeds that of their cebine sister taxa, i.e. capuchin and squirrel monkeys. Even though each single comparison must be considered preliminary due to the lack of uniformity in experimental procedures, we found no exceptions to this general pattern, i.e. no task in the social domain in which cebines unambiguously outperformed the callitrichids. Given that the reproductive system of capuchin monkeys is intermediate between callitrichids and squirrel monkeys with regard to allomaternal care, one would also predict that they are intermediate in the present comparison.

While this seems to be true for spontaneous prosociality, there are not enough data available to date for socio-cognitive performance and direct tests based on exactly the same methods are necessary.

The callitrichids' enhanced cognitive performance in social domains can reasonably be attributed to the presence of motivational and cognitive processes that are involved in the regulation of the callitrichid breeding system, such as attentional biases, high social tolerance and spontaneous prosociality, and that are also recruited in experimental socio-cognitive tasks. At the same time, callitrichids consistently performed more poorly than capuchin monkeys, and, to a lesser extent, than squirrel monkeys, in the physical domain. Poorer performance in the physical domain is consistent with the fact that callitrichids have smaller brains compared to their sister taxa (Herculano-Houzel et al. 2007) and that performance in such tasks is directly related to absolute brain size (Deaner et al. 2007).

We complemented this systematic comparison with a qualitative survey of prosociality and cognitive performance of cooperative breeders among non-primate mammals. The findings for these taxa support the conclusions drawn for the callitrichids, although obviously future studies are required that contrast non-primate species that rely on extensive allomaternal care with their independently breeding sister taxa in order to deal with the effect of confounding factors.

Cooperative breeding and the cultural intelligence hypothesis

According to the cultural intelligence hypothesis in its general form (van Schaik 2004; Whiten and van Schaik 2007; van Schaik and Burkart 2009b; for its specifically human version, see Herrmann et al. 2007), one would expect that an increase in social learning leads to concomitant effects on other cognitive abilities. Whereas this study found this holds for the socio-cognitive abilities, it also points to a dissociation between social learning and performance in non-social tasks. The increased socio-cognitive performance of callitrichids most plausibly is a direct reflection of the more favorable conditions such as increased social tolerance and attentional biases towards the behavior of others, rather than the emergence of new, genetically anchored cognitive abilities. The question whether increased performance in socio-cognitive tasks in callitrichids is also accompanied by increased or even qualitatively new cognitive abilities requires careful analysis in every single case. Such analyses (Burkart and Heschl 2007; Burkart et al. 2009), as well as the lack of a concomitant increase in the non-social domain, suggest that the improved performance in social cognition in callitrichids is due to external (close and relaxed proximity to other group members) and internal (presence and strength of motivational and cognitive processes involved in the regulation of helping behaviors, see above) facilitating conditions, and not due to improved cognitive abilities per se.

The view that individuals experiencing favorable social conditions show superior performance in various social tasks is not new (e.g. the role of social tolerance in performance in social learning: Coussi-Korbel and Fragaszy 1995). It is also consistent with results from Japanese monkeys (*Macaca fuscata*), for whom under naturalistic conditions no evidence for imitational learning is available. Monkeys were rigorously trained to engage in joint attention and subsequently showed imitative performance of hand-movements and actions on objects (Kumashiro et al. 2003). Hence, an attentional bias toward monitoring the behavior of others, similar to the one present in callitrichids due to the requirements of cooperative breeding, was induced experimentally in these Japanese macaques and resulted in enhanced performance in imitation.

Nevertheless, the question remains why the coevolutionary process proposed by the cultural intelligence hypothesis was not released in callitrichids, because increased performance might translate into increased survival and reproduction independent of the mechanism responsible for this increase. The reason is that the cultural intelligence hypothesis is a cost hypothesis, proposing that the presence of social learning decreases the costs of developing bigger brains. Thus, if the costs are very high, the threshold for releasing a coevolutionary process might be more difficult to reach. The costs may be high in callitrichids, because they are small species under high predation pressure, as compared to other non-human primates. Increased brain size would lead to delayed maturation, thus probably imposing a non-sustainable demographic cost (Barrickman et al. 2008; Isler and van Schaik 2009), because callitrichids may not be able to turn enhanced non-social cognitive abilities into the necessary improvement in adult survival, given the presence of many large predators. The coevolutionary processes between social learning and individual cognitive ability should be more powerful in species that already show ecological and life history traits favorable to the evolution of bigger brains, such as hominoids (Kelley 2004).

The role of cooperative breeding during human cognitive evolution

The cognitive abilities of humans are markedly different from those of our closest relatives, the great apes, and the Cooperative Breeding Model proposed by Hrdy (1999, 2005a, b, 2009) suggests that these differences might be due extensive allomaternal care which is present in humans, but not in great apes. Do the results of our comparison support this hypothesis? In callitrichids, and presumably in canids and elephants as well, reliance on extensive allomaternal care is associated with improved performance in socio-cognitive contexts, despite differences in the details of their breeding systems. In the hominin lineage, however, the adoption of this breeding system would have to explain more far-reaching cognitive consequences (Burkart et al. 2009b). We suggest that this became possible because in our lineage, cooperative breeding was added to an already ape-level cognitive system, able to understand mental states, at least in competitive contexts (Call 2007). As a direct consequence, engaging in extensive allomaternal care allowed deploying already present cognitive abilities in cooperative contexts as well. In addition, the associated prosocial motivations could not only be applied to food and maybe information, as is the case in callitrichids who show active provisioning and information donation, but also to mental states such as perceptions and attention, thus allowing the evolution of shared intentionality with all its cognitive consequences. Recent proposals indeed view shared intentionality as the root of the differences between human and great ape cognition (Tomasello and Rakoczy 2003; Tomasello et al. 2005). Thus, in callitrichids, extensive allomaternal care primarily has motivational correlates that as a side-effect translate to some increased performance in socio-cognitive contexts. In humans, however, the same motivational correlates were added to a more sophisticated cognitive system, which had the potential to release a whole cascade of events resulting in the emergence of uniquely human cognition (Tomasello and Carpenter 2007; Burkart et al. 2009b).

In sum, we argue that while chimpanzees and maybe all great apes (e.g. Call 2007; Deaner et al. 2006) may have many of the important *cognitive* preconditions for uniquely human cognition to evolve, callitrichids possess the *motivational* requirements. In humans, 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 extensive allomaternal care (Burkart et al. 2009b).

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