

MINI-SERIES

Cognitive consequences of cooperative breeding? A critical appraisal

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Keywords

cognition; cooperative breeding hypothesis; social intelligence hypothesis; prosociality; social learning; teaching; behavioural coordination.

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Editor: Heike Lutermann

Received 27 May 2014; revised 13 August 2014; accepted 23 September 2014

doi:10.1111/jzo.12198

Introduction

Struck by the complex social manoeuvrings of their study species, early pioneers in primatology suggested that the social world, rather than the physical environment, generates the selective pressures driving the evolution of primate brains and cognition (Chance & Mead, 1953; Jolly, 1966). This idea, later elaborated by Nick Humphrey (1976), came to be known as the social intelligence hypothesis and now enjoys widespread support as the dominant explanation for cognitive evolution in vertebrates (Dunbar, 1998; Emery, Clayton & Frith, 2008; but see Holekamp, 2007 for an appraisal of the limitations of the hypothesis). Across primates, other mammals, birds and even fish, a wealth of evidence indicates that social life, particularly where it features individualized relationships, is associated with enhanced cognitive abilities (Cheney & Seyfarth, 2007; Connor, 2007; Emery et al., 2007; Bshary, Gingins & Vail, 2014) and enlarged brains (Dunbar & Shultz, 2007; although see Healy & Rowe, 2007 for a critique of comparative studies of brain size). In recent years, Burkart, Hrdy and colleagues have proposed a novel variant of the social intelligence hypothesis, emphasizing cooperative breeding as a central driver of enhanced cognitive abilities (Burkart, Hrdy & Van Schaik, 2009; Hrdy, 2009; Burkart & van Schaik, 2010; see also Snowdon, 2001). According to this hypothesis, cooperative breeding, a social system in which group members

Abstract

The social intelligence hypothesis, which posits that the challenges of life in complex social environments drive cognitive evolution, enjoys widespread theoretical and empirical support. Recent years have seen the emergence of a novel variant of this hypothesis, suggesting that cooperative breeding is associated with the elaboration of socio-cognitive abilities. With this cooperative breeding hypothesis (CBH) rapidly gaining currency, the time is ripe for a critical appraisal. Proponents of the CBH argue that cooperative breeding leads to increased cognitive performance, calling upon cognitive and motivational processes including spontaneous prosocial tendencies, attending to and learning from conspecifics, teaching and coordinating activities. We review the literature on the natural history and cognitive abilities of cooperative breeders and other social animals and conclude that there is no compelling evidence that these processes are either unique to cooperative breeders or particularly cognitively demanding. Thus, there is currently no reason to suppose that cooperative breeding has major cognitive consequences.

termed helpers assist in caring for offspring that are not their own, is associated with enhanced social motivations and socio-cognitive skills. This association is varyingly framed either as a byproduct of other characteristics of cooperatively breeding species, such as social tolerance (Burkart et al., 2009, p. 14), or as an adaptation to specific challenges faced by cooperative breeders (e.g. Burkart & van Schaik, 2010, p. 12). Critically, both versions of the hypothesis claim that cooperative breeding has consequences for social cognition and may account for the emergence of unique traits such as shared intentionality and theory of mind in humans (Burkart et al., 2009; Hrdy, 2009). With this cooperative breeding hypothesis (CBH) rapidly gaining currency in the ethological, psychological and anthropological literature (>150 citations for Burkart et al., 2009 and Burkart & van Schaik, 2010 in Google scholar at the time of writing), the time is ripe for a critical appraisal.

The comparative case for the CBH rests largely on the claim that callitrichid monkeys outperform closely related independently breeding species (particularly capuchins, *Cebus* spp., and squirrel monkeys, *Saimiri* spp.) in socio-cognitive tasks. This narrow taxonomic focus is problematic for two main reasons. First, as *all* callitrichids are cooperative breeders, there is no scope for phylogenetically controlled within-family analyses of behavioural or cognitive variation. Second, as callitrichids are the *only* cooperatively breeding non-human primates, the comparison is forced to rely on a narrow sliver of the comparative cognition literature, rendering it difficult to draw robust conclusions. To evaluate the plausibility of the CBH, we review the neuroanatomical, behavioural and cognitive literature across cooperative breeders and other social animals. We conclude that there is little evidence to suggest that cooperative breeding entails distinct cognitive challenges or has important cognitive consequences.

Is cooperative breeding related to brain size?

Among the most widely cited evidence for the social intelligence hypothesis is the relationship between measures of social complexity and brain size. Among primates, Dunbar (1998) famously argued that species living in large groups would face substantial cognitive challenges arising from the need to recognize and remember multiple group members, anticipate their actions and track their relationships. Accordingly, he found a strong positive relationship between average group size across species and the relative volume of the neocortex, the supposed seat of higher cognitive function and the brain area that has been most expanded in primates (Dunbar, 1998; Dunbar & Shultz, 2007). In other taxa including bats, ungulates, mammalian carnivores and birds, relationships between brain size and sociality appear to hinge not on group size, but on the occurrence of long-term, monogamous pair bonds (Dunbar & Shultz, 2007; Emery et al., 2007; Shultz & Dunbar, 2010). This effect holds even in artiodactyl ungulates, where males do not contribute to parental care, suggesting that pair bonding per se, as opposed to biparental care, may be the causal factor driving brain size evolution in non-primates (Dunbar & Shultz, 2007). Unlike social primates, which typically face demands of managing multiple relationships, the cognitive challenges in other taxa are argued to centre on relationship quality rather than quantity, through the demands of choosing a high-quality partner, coordinating activities and providing mutual support (Emery et al., 2007; Shultz & Dunbar, 2007). Across all these taxa, however, it seems clear that the occurrence of individualized relationships is associated with cognitive challenges and brain evolution.

In accordance with 'social brain' arguments, one might suppose that if cooperative breeding generates distinctive cognitive challenges, these too may result in selection for large brains or brain components. In fact, there is no evidence to suggest that this is the case. In the only explicit study of brain size in relation to cooperative breeding, using a sample of 155 birds from the avian Corvida parvorder, Iwaniuk & Arnold (2004) found no relationship. Among primates, the cooperatively breeding callitrichids are notable for their small brains, which are between four and seven times smaller than those of their 'sister' groups, the squirrel monkeys and capuchins (Herculano-Houzel et al., 2007). In a dataset of 37 simian primates complied by Reader & MacDonald (2002), callitrichid species occupied five of the six bottom places in terms of absolute brain mass, relative neocortex size and executive brain ratio, suggesting that cooperative breeding is not linked to brain size.

Proponents of the CBH make the rather paradoxical claim that small brain size in callitrichids supports their hypothesis because these monkeys manage to show impressive sociocognitive skills despite their small brains. Thus, cooperative breeding *per se* is argued to generate elevated socio-cognitive performance even though given their small brains 'one would expect that callitrichids have far less elaborate cognitive abilities than their [independently breeding] sister groups' (Burkart & van Schaik, 2010, p. 5). This view is problematic for three reasons. First, it is in direct conflict with traditional 'social brain' arguments, which indicate that brain size should increase as a function of socio-cognitive demands (Dunbar, 1998; Dunbar & Shultz, 2007). Second, it also contrasts with work suggesting that allomaternal care in birds and some mammals reduces energetic constraints and so permits the growth of larger brains (Isler & van Schaik, 2009, 2012). With regard to this issue, it important to note that relationships between allomaternal care and brain size (1) do not hold among primates; (2) typically include contributions by fathers and so are not specific to cooperative breeders, where nonparents contribute to offspring care; and (3) arguments based on reduction of energetic constraints cannot explain why larger brains would be subject to positive selection (Dunbar, 1998). Finally, the view that cooperative breeders show sociocognitive prowess despite their small brains places the burden of evidence firmly on the claim that cooperative breeders do in fact show elevated socio-cognitive performance. It is to this claim that we now turn our attention.

Does cooperative breeding entail distinct socio-cognitive challenges?

According to some versions of the social intelligence hypothesis, the challenges of sociality may select not only for cognitive abilities in the social domain, but also for elevated 'general intelligence' across contexts (see Whiten & Byrne, 1988; Whiten & van Schaik, 2007). This does not seem to apply to cooperatively breeding callitrichids as meta-analyses of cognitive performance across contexts indicate that these species show among the lowest levels of general intelligence among primates (Deaner, van Schaik & Johnson, 2006; Reader, Hager & Laland, 2011). Instead, the challenges of cooperative breeding may be manifested in the elaboration of more specific socio-cognitive skills.

In the broader literature on social intelligence, there are strong indications that social animals tend to show elevated socio-cognitive performance compared with less social species (Byrne & Whiten, 1988; Cheney & Seyfarth, 2007). For instance, social species of corvids and prosimian primates do better than related, less social species in tests of transitive inference, an ability which may assist in predicting the relative ranks of other individuals in hierarchically structured social groups (Bond, Kamil & Balda, 2003; Maclean, Merritt & Brannon, 2008). Is there any evidence that similar sociocognitive differences might occur between cooperative breeders and independent breeders?

Many of the central cognitive demands highlighted by the social intelligence hypothesis seem less relevant to cooperative

breeders than to many other independently breeding social species. In particular, the social intelligence hypothesis often emphasizes social flexibility and Machiavellian strategizing in highly individualized, dynamic societies such as multi-male, multi-female groups of mixed kinship and groups with fission-fusion social dynamics (Byrne & Whiten, 1988; de Waal & Tyack, 2003; Barrett, Henzi & Lusseau, 2012). In contrast, cooperative breeders tend to live in comparatively simple kin-based groups where the main social distinction is between older, larger breeders and vounger, smaller, nonbreeding helpers (Stacey & Koenig, 1990; Solomon & French, 2007) and there is little evidence for individualized relationships and little scope for non-breeders to negotiate or influence access to resources or reproductive opportunities (Kutsukake & Clutton-Brock, 2008), Nevertheless, the proponents of the CBH argue that cooperative breeding leads to elevated performance in certain socio-cognitive traits, particularly with regard to prosociality, social learning, teaching and behavioural coordination (Burkart & van Schaik, 2010). We now consider each of these claims in turn.

Prosociality

One of the central claims of the CBH is that cooperative breeding entails 'prosocial' tendencies [voluntary behaviours that benefit others; (Jensen, Vaish & Schmidt, 2014)] that are not present in independent breeders and that such tendencies are largely responsible for the unique socio-cognitive characteristics of humans (Burkart *et al.*, 2009; Burkart & van Schaik, 2010). This argument stems largely from the observation that, unlike other primates, callitrichid monkeys often donate food voluntarily to conspecifics, which is taken to indicate a psychological concern for the welfare of others.

However, under natural conditions, callitrichid food donation is almost exclusively from adults to dependent young (Izawa, 1978; Rapaport & Ruiz-Miranda, 2006) and so is equivalent not only to offspring provisioning in other cooperative breeders, but also in independent breeders including, for example, mammalian carnivores such as felids and the vast majority of birds (Clutton-Brock, 1991; Cockburn, 2006). Non-reproductive helpers in cooperatively breeding groups are typically related to offspring and provisioning by parents and helpers is largely under hormonal control, as is also the case for parental care in independent breeders (see Soares *et al.*, 2010). Thus, there is little reason to suppose that provisioning by parents and helpers differs fundamentally in terms of psychological mechanisms.

Callitrichids, in common with parents and helpers in other taxa, commonly provision young in response to begging calls (Brown, Almond & Bates, 2005), but may also provide food in the absence of overt begging signals or harassment by offspring. The prevalence of such 'unsolicited provisioning' is variable [estimates from captive groups range from 1.5% of all donated food items in pied bare-faced tamarins *Saguinus bicolor* (Price & Feistner, 2001) to 27.6% in cotton-top tamarins *Saguinus oedipus* (Feistner & Price, 1990)] but the proponents of the CBH place great emphasis in its occurrence as evidence for what they term 'proactive prosociality'

(Burkart & van Schaik, 2010; Jaeggi, Burkart & Van Schaik, 2010) akin to the concern for others found in human societies. However, this view ignores the fact that adults are hormonally primed to feed the offspring and that offspring's physical characteristics themselves induce (allo)parental behaviour even in the absence of begging (Storey et al., 2000; Angelier & Chastel, 2009; Barbosa & da Silva Mota, 2013). In addition, numerous studies have shown that adults' contributions to offspring care are conditional, varying in response to factors such as their own condition and the strength of signals from offspring (Heinsohn & Legge, 1999; Clutton-Brock et al., 2001, 2005; Bell, 2010). Thus, rather than being driven by a general psychological motivation for generosity, it seems that parents and helpers selfishly adjust their contributions to maximize their own direct and indirect fitness benefits. Moreover, cooperative breeders are certainly not alone in feeding young in the absence of overt signals of solicitation. Independently breeding passerine birds, for instance, commonly forage out of earshot of nestlings, bring food back to the nest and then produce distinctive food calls to elicit begging and acceptance of food by chicks (Leonard, Fernandez & Brown, 1997; Madden, Kilner & Davies, 2005; Zandberg et al., 2014). Thus, natural history provides little evidence that patterns of food sharing by callitrichids or other cooperative breeders are fundamentally distinct to those found in other social species either in frequency or mechanistic underpinning.

Nevertheless, studies of free-living animals cannot easily pinpoint underlying motivational processes, so numerous experimental studies have attempted to test whether animals show prosocial tendencies under controlled laboratory conditions. In these tests, a donor animal generally pulls an apparatus that will deliver food rewards to itself and/or to a conspecific in an adjacent cage in situations with differing payoff distributions. The precise methodologies employed in different studies vary substantially, making it difficult to draw clear conclusions regarding differences between species (see McAuliffe & Thornton, 2014 in this issue and Burkart et al., 2014), but the proponents of the CBH argue that cooperatively breeding callitrichids tend to be more prosocial than other primates. For instance, Burkart et al. (2007) found that common marmoset Callithrix jacchus donors preferred to pull a tray if it delivered one food item to a neighbour but none to themselves (0,1 payoff) rather than no reward for either individual (0,0). They contrasted this with results from earlier studies indicating that chimpanzees Pan troglogytes do not provide food for others at no cost to themselves (Silk et al., 2005; Jensen et al., 2006) and proposed that their marmosets' behaviour reflects prosocial tendencies arising from cooperative breeding. However, this interpretation is problematic for a number of reasons. First, while some other studies on callitrichids have found similar prosocial effects (Cronin, Schroeder & Snowdon, 2010; Burkart & van Schaik, 2013), others have not (Cronin et al., 2009; Stevens, 2010). Second, a number of studies on independently breeding primates including chimpanzees (Warneken & Tomasello, 2006; Warneken et al., 2007; Greenberg et al., 2010), longtailed macaques Macaca fascicularis (Massen et al., 2010) and capuchins (Lakshminarayanan & Santos, 2008) also claim to have evidence for prosociality, undermining the argument that such tendencies are unique to cooperative breeders.

Perhaps the strongest evidence for a link between cooperative breeding and prosociality comes from recent work by Burkart et al. (2014). They used a 'group services' paradigm to test captive groups of 14 non-human primate species as well as human children, employing the same methods across species to allow meaningful comparisons. Unlike previous studies, this paradigm did not use actor-recipients dyads in separate cages but instead allowed individuals within groups to choose to pull a tray to make food accessible to other group members but not themselves (0,1 rewards). Measures of 'proactive prosociality' were positively correlated with social tolerance and pair bonding and negatively correlated with brain size, but the strongest predictor was the extent of allomaternal care in each species. This result appears consistent with the CBH, but a number of important issues remain unclear. First, the implications for our understanding of the consequences cooperative breeding per se are limited because only primates were tested and of the non-human species included only three callitrichid species were true cooperative breeders, where nonparents contribute to offspring rearing. We also note that the variation in prosociality among the five marmoset groups tested was similar to the total variation between species. Second, a number of methodological issues make it difficult to assess the robustness of the results. The experiment was run over a number of phases. These were designed to test subjects' understanding of task contingencies, but as they were run in sequence it is difficult to discount order effects. The main experimental trials were run in phase IV, when pulling made food available to others. In the subsequent phase V, recipients' access to the food was blocked by a mesh; sustained pulling in this stage would indicate that actors were not motivated by the aim of delivering food to others. Most individuals showed lower pulling rates in phase V (0,0) than phase IV (0,1), suggesting that they preferred to pull if others were rewarded. However, as phase V was run after phase IV it is also possible that the pattern results from a decline in motivation to pull over the course of the experiment. Moreover, the measure of 'proactive prosociality' used as the response term in analyses was the proportion of trials in which individuals delivered food to others in phase IV. Arguably a clearer measure of prosociality would be the difference in pulling between phases IV and V (i.e. the preference for assisting others, over and above baseline tendencies to pull when rewards were visible), but as phase V was only conducted on species that showed sustained levels of pulling in phase IV, such analyses were not possible. Thus, while the results are suggestive and testing different species with the same paradigm is clearly an important methodological advance, the implications of Burkart et al.'s (2014) study remain somewhat questionable.

Finally, there are strong reasons to doubt the theoretical claim that prosocial tendencies in laboratory experiments reflect high rates of food sharing in the wild. Not only is food sharing in callitrichids and other cooperative breeders generally limited to provisioning of dependent young rather than sharing among adults, but a recent study on a species which does show high levels of food sharing across contexts failed to find evidence for prosocial tendencies. Jackdaws Corvus monedula, an independently breeding, colonial corvid species, share food at higher rates and with a wider range of partners than any primate, including from parents to offspring, between mating partners and among non-relatives (de Kort. Emery & Clayton, 2006; von Bayern et al., 2007), but nevertheless were significantly more likely to choose selfish (1,0) than generous (1,1 or 0,1) options in a laboratory task (Schwab et al., 2012). It is also important to note that, whereas food-donating animals and human subjects in economic games such as the dictator game must give away a resource they have already acquired, existing tests of animal prosociality require no such sacrifice of personal gain. As there is no clear cost to the donor of choosing one option over another (i.e. they can never end up worse off than they were before), it is not clear that such studies truly shed light on seemingly altruistic forms of human behaviour in which people willingly incur costs to help others (see also McAuliffe & Thornton, 2014).

Social learning

Along with strong prosocial tendencies, human societies are characterized by highly diverse and complex forms of culture - group-typical forms of behaviour that arise as a result of the spread of information through social learning (Richerson & Boyd, 2005). The spread and elaboration of knowledge and skills through social learning is widely acknowledged to have a profound influence on the evolutionary dynamics and ecological success of human populations and so efforts to uncover the biological origins of culture have become a major focus of comparative research (Richerson & Boyd, 2005; Whiten et al., 2012). According to proponents of the CBH, cooperative breeding played a key role in the emergence of human culture and is associated with an increased prevalence of social learning in other taxa (Burkart et al., 2009; Burkart & van Schaik, 2010). Is there any theoretical rationale for assuming that social learning should be particularly prevalent in cooperative breeders and does the empirical data support this notion?

Theory suggests that animals should rely on social learning particularly when individual learning is costly (Boyd & Richerson, 1985). Animals that must, for example, learn to recognize and respond appropriately to predators, discriminate between edible and toxic food sources or catch dangerous prey would thus be expected to rely heavily on social learning, irrespective of their particular breeding system. Meerkats Suricata suricatta, for instance, rely on social learning for the acquisition of anti-predator and foraging skills because they are generalist carnivores living under high predation pressure, not specifically because they are cooperative breeders (Thornton & Clutton-Brock, 2011). Burkart et al. (Burkart et al., 2009; Burkart & van Schaik, 2010) argue that, compared with independent breeders, cooperative breeders may have additional opportunities to attend to and learn from others because they have greater levels of social tolerance. However, it is not clear whether cooperative breeders are generally more socially tolerant than other social animals, as data for systematic comparisons are lacking. While cooperative

breeders do often aggregate and forage in close proximity with little conflict, so do many independently breeding species including many birds (Emery *et al.*, 2007; Dardenne *et al.*, 2013), cetaceans (Sargeant & Mann, 2009) and primates such as bonobos *Pan paniscus* (de Waal, 1989). Moreover, despite high levels of cooperation, life in many cooperatively breeding societies is punctuated by regular bouts of violent conflict over access to resources and mating opportunities (Clutton-Brock, 1998).

We see few theoretical reasons to expect social learning to be particularly prevalent in cooperative breeders, but does the empirical literature support the contention? Burkart & van Schaik (2010) base their claim largely around the literature survey by Custance, Whiten & Fredman (2002) which collated results from studies of social learning in the wild and in captivity from 1950 to 2002 and found five out of five studies on callitrichids but only 10 out of 23 studies on cebids reported evidence for social learning. However, many of these studies did not disentangle social from individual learning. If we include only the papers classified by Custance et al. (2002) as showing 'strong' evidence for social learning (i.e. including experimental treatments to control for individual learning), there is no detectable difference between callitrichids (three out of five) and cebids (six out of 23) ($\chi^2 = 2.17$; P = 0.141). It is also worth noting that the occurrence of social learning in artificial laboratory conditions may not reflect its preponderance under natural conditions. There have been relatively few systematic studies of social learning in wild animals, but the majority of the evidence suggests that among both cooperative and independent breeders, social learning is used primarily as a means for young individuals to acquire adaptive information from their elders, be these parents or alloparents (Thornton & Clutton-Brock, 2011). In a comprehensive survey of reports of social learning in the primatological literature, corrected for research effort, Reader (2003) found considerably lower rates of social learning in callitrichids than capuchins: while Cebus apella ranked third out of 32 primate species (behind chimpanzees and orangutans *Pongo pygmaeus*), the callitrichids Saguinus oedipus, Saguinus midas and Callithrix jacchus ranked 10th, 16th and 24th, respectively.

Casting the taxonomic net beyond primates further weakens the argument that social learning is associated with cooperative breeding. For instance, Burkart & van Schaik (2010) highlight studies showing that social learning promotes the acceptance of novel foods by callitrichids but not capuchins, but they do not consider the broader literature. While it is certainly the case that juveniles in generalist cooperatively breeding species, such as meerkats, learn about novel foods from their elders (Thornton, 2008a), so do a host of independent breeders including vervet monkeys, rats, sheep, chickens and ptarmigans (Thorhallsdottir, Provenza & Balph, 1990a; Gerrish & Alberts, 1995; Sherwin, Heyes & Nicol, 2002; Allen & Clarke, 2005; van de Waal, Borgeaud & Whiten, 2013; see Galef & Giraldeau, 2001 for a review). Similarly, while Burkart & van Schaik (2010) emphasize the finding that callitrichids but not capuchins learn to avoid noxious foods through social learning, they fail to note that socially learned food avoidance has also been documented in lambs Ovis aries

(Thorhallsdottir, Provenza & Balph, 1990b) red-winged blackbirds *Agelaius phoeniceus* (Mason, Arzt & Reidinger, 1984) and day-old chicks *Gallus gallus domesticus* (Johnston, Burne & Rose, 1998). Thus, the empirical data does not appear to support the argument that cooperative breeding leads to more social learning.

Instead, perhaps social learning in cooperative breeders might employ different underlying mechanisms from that in other species. The prevailing consensus is that social learning relies on general learning mechanisms that are taxonomically widespread throughout invertebrates and vertebrates (Heyes, 2012; Dawson et al., 2013). Nevertheless, it is possible that certain specialized mechanisms are better developed or more widely used by cooperative breeders. Psychologists have long focused on imitation as a cognitively challenging form of social learning, as imitators are thought to face the 'correspondence problem' of matching their own body actions to those of another (Zentall, 2012). Some cooperative breeders have indeed proven to be adept imitators. Marmosets, for instance, copied the actions of a trained demonstrator, opening a container either with their hands or with their mouth (Voelkl & Huber, 2000). Wolves Canis lupus and dogs Canis familiaris (which in their ancestral form might be argued to be cooperative breeders) have shown similar aptitudes (Range, Huber & Heyes, 2011; Range & Virányi, 2014). However, this ability does not appear to be general to cooperative breeders: systematic analyses of meerkat social learning mechanisms under natural conditions revealed no evidence for imitation (Hoppitt et al., 2012). Moreover, numerous independently breeding birds and mammals are also known to imitate (Zentall, 2006; Byrne, 2009; Huber et al., 2009). Thus, imitation does not seem to be strongly associated with cooperative breeding.

Teaching

While cooperative breeders do not obviously stand out as social learners, perhaps they stand out as teachers. Teaching, unlike other forms of social learning, involves an active investment by knowledgeable individuals in facilitating learning by the naïve (Caro & Hauser, 1992; Thornton & Raihani, 2008). According to the CBH, teaching is 'strikingly overrepresented' in cooperative breeders and is yet another example of these animals' 'increased cognitive performance' (Burkart *et al.*, 2009). This conclusion appears premature at best.

First, there is no reason to treat teaching as indicative of high cognitive performance, as existing work suggests that non-human animal teaching is governed by simple processes and does not involve mechanisms such as metacognition and theory of mind that underpin some forms of human teaching (Thornton & McAuliffe, 2012). Adult meerkats, for instance, teach pups how to hunt through reflexive responses to agerelated changes in pups' begging calls, bringing dead prey in response to the calls of young pups and live prey when they hear old pups (Thornton & McAuliffe, 2006).

Second, current evidence and theory does not point to a clear overrepresentation of teaching among cooperative breeders. While the three species for which there is strong experimental evidence of teaching – meerkats, pied babblers Turdoides bicolor and tandem running ants Temnothorax albipennis - are all cooperative breeders (Franks & Richardson, 2006; Thornton & McAuliffe, 2006; Raihani & Ridley, 2008), this may well reflect their tractability as study systems, as opposed to a general property of cooperative breeders. Among callitrichids, for example, the evidence for teaching is equivocal. Some researchers have suggested that adults teach juveniles to recognize and acquire new foods by preferentially donating novel or hard-to-process items and using calls to attract juveniles to foraging sites (Rapaport, 1999, 2011). However, other studies have found that adults are less likely to donate novel than familiar items (Price & Feistner, 1993; Brown et al., 2005) and to date there is no evidence that young callitrichids learn as a result of adult behaviour. It therefore remains unclear whether patterns of provisioning are driven by youngsters' nutritional or informational needs. In the context of teaching about novel foods, the strongest evidence is arguably from independently breeding white-tailed ptarmigans Lagopus leucura, where the frequency of mothers' feeding displays towards high protein plants is positively correlated with the chicks' incorporation of these plants into their diet (Allen & Clarke, 2005). Looking across contexts, the quality of evidence for teaching among callitrichids is comparable with that for several independently breeding primates, for which there are putative examples of adults teaching infants to locomote independently (Maestripieri, 1995) and even use human hair as dental floss (Masataka et al., 2009). Across all taxa, a comprehensive review reported some evidence (mostly inconclusive) for teaching from 42 species, of which only seven were cooperative breeders (Thornton & Raihani, 2008).

From a theoretical perspective, there is no clear reason to expect that cooperative breeding is either sufficient or necessary for teaching to evolve. Teaching will only be favoured by selection if the short-term costs incurred by teachers when helping pupils to learn are outweighed by the long-term benefits once pupils have learned (Thornton & Raihani, 2008; Fogarty, Strimling & Laland, 2011). In cooperative breeders, two factors may help to tip the cost-benefit balance in favour of teaching. First, adults may gain both direct benefits (e.g. by augmenting group size and so reducing the risk of predation) and indirect, kin-selected benefits by helping related young acquire important skills. Second, the costs of teaching are divided among multiple helpers (Thornton, 2008b). However, these factors alone cannot account for the evolution of teaching, because teachers' fitness payoffs must be scaled by the utility of the information to be learned. Utility is particularly high when naïve individuals cannot easily learn critical skills through trial and error or by observing others, as is the case for solitary hunters. Accordingly, much of the strongest evidence for teaching comes from felids where, like adults in meerkat societies, mothers provide cubs with otherwise unavailable opportunities to handle live prey (reviewed in Thornton & Raihani, 2008). In contrast, in group hunting canids, many of which are cooperative breeders, the young can learn through direct experience from joining hunts, which may explain the lack of evidence for teaching in this taxon

(Thornton & Raihani, 2008). In sum, therefore, current evidence indicates that teaching is neither intrinsically cognitively demanding nor overrepresented in cooperative breeders.

Behavioural coordination

Finally, we consider the CBH's contention that cooperative breeders show distinct cognitive and motivational biases for coordinating cooperative activities (Burkart & van Schaik, 2010). While callitrichid monkeys and other cooperative breeders may coordinate contributions to behaviours such as vigilance, territory defence and the care of young, the same is also true of other social animals. For example, the use of sentinels that scan for danger and alert other group members is common not only in cooperative breeders but also in independently breeding social birds and mammals, including primates such as vervet monkeys Chlorocebus pygerythrus and baboons (Papio spp.) (reviewed in Bednekoff, 1997). Similarly, communal territory defence occurs both in cooperative breeders [e.g. marmosets (Lazaro-Perea, 2001), meerkats (Jordan, Cherry & Manser, 2007), green woodhoopoes Phoeniculus purpureus (Radford, 2003)] and other groupliving species [e.g. striped mice Rhabdomys pumilio (Schradin, 2004), vervet monkeys (Cheney, 1992) and chimpanzees (Williams et al., 2004)]. Finally, coordination and negotiation over contributions to offspring care are likely prevalent both in cooperative breeders and in species with biparental care of young. Birds such as great tits Parus major, for example, adjust their provisioning rates in response to their partners' efforts and signals from the brood (Hinde & Kilner, 2007).

Cooperative breeders might face particular cognitive challenges if, for example, dominant individuals must keep track of the relative contributions of multiple group members to cooperative activities. According to the pay-to-stay hypothesis, helpers cooperate as payment for the right to reside on a territory and breeders enforce cooperation by attacking lazy helpers (Gaston, 1978). However, support for this hypothesis is limited and controversial (Raihani, Thornton & Bshary, 2012; Santema & Clutton-Brock, 2012). The strongest evidence comes from experiments on cooperatively breeding cichlid fish Neolamprologus pulcher, where individuals that were prevented from helping by temporary removal from the group were subsequently attacked by other group members (Balshine-Earn et al., 1998). However, this effect might be explained by disruption to dominance relations resulting from the temporary removal. In another experiment where helpers remained in the group, dominants did not attack helpers that were experimentally prevented from helping (Bergmüller & Taborsky, 2005; see Santema & Clutton-Brock, 2012 for a similar result in meerkats). To date, there is no clear evidence from any species that dominants keep tabs on individual helpers' contributions to offspring care.

While the coordination of cooperative activities is clearly not limited to cooperative breeders, perhaps these species employ more cognitively taxing forms of coordination than those used by other animals. Burkart & van Schaik (2010) point to the transfer of infants between helpers in callitrichid societies as requiring precise spatial and temporal coordination so as to avoid dropping the hapless infant to the ground. However, it is not clear why this behaviour ought to be considered any more impressive than any other instance in which objects are passed between individuals, such as egg transfers from mother to father in Emperor penguins (Williams, 1995), or transfers of food and other objects during offspring provisioning, courtship feeding and social play across many taxa (Shimada, 2006; von Bayern *et al.*, 2007). More generally, there is extensive evidence that seemingly complex forms of behavioural coordination such as the spectacular formations of flocking birds and schooling fish can arise as emergent properties of groups in which individuals follow simple rules (Sumpter, 2006). Thus, we can see little reason to suppose that coordination in cooperative breeders is cognitively taxing.

One may argue that more complex forms of coordination are required when individuals have to work together to achieve a joint aim. Cooperative hunting, for instance, may require individuals to attend to and respond flexibly to the actions of others and, arguably, to recognize when assistance is needed. However, while some cooperative breeders such as African wild dogs Lycaon pictus are cooperative hunters (Creel & Creel, 1995), most cooperative breeders are not. Moreover, the occurrence of cooperative hunting among, for example, chimpanzees (Boesch, 1994), dolphins (e.g. Tursiops truncatus; Gazda et al., 2005) and in interspecific interactions between moray eels Gymnothorax javanicus and grouper fish Plectropomus pessuliferus (Bshary et al., 2006) illustrates that such coordination is not restricted to cooperative breeders. A number of experimental studies have tested the cognitive requirements of coordination during cooperative problemsolving tasks, but again these provide little evidence of superiority among cooperative breeders. Cronin, Kurian & Snowdon (2005), for instance, found that pairs of cotton-top tamarins could work together to pull two ends of a rope to access a tray with food and were likely to pull when their partner was present than when alone, indicating they recognized the need for help (Cronin et al., 2005). However, the fact that the monkeys did occasionally pull in the absence of a partner casts some doubt on this interpretation and the results could be explained by the use of a simple learned rule (e.g. 'pull when partner present'; see Noë, 2006 for a critical analysis of this and other similar studies). While it is difficult to make precise comparisons between studies because of methodological differences, current data suggest that, as one might expect, species that engage in cooperative hunting, such as chimpanzees and spotted hyenas Crocuta crocuta, tend to do particularly well in cooperative tasks (Melis, Hare & Tomasello, 2006; Drea & Carter, 2009). For example, experiments have convincingly demonstrated that chimpanzees understand the causal role of their partner in cooperative problem-solving tasks and strategically recruit effective partners when needed (reviewed in Melis, 2013).

Conclusion

The precise logical formulation of the CBH is variable. At times it is phrased as an adaptive hypothesis, suggesting that selection favours socio-cognitive skills in response to the challenges of cooperative breeding. Burkart & van Schaik (2010), for example, mention 'specific socio-cognitive adaptations to cooperative breeding' (p. 12) and 'selection pressures associated with extensive allomaternal care' (p. 14). More often, increased cognitive performance is said to arise as a 'sideeffect' of cooperative breeding (Burkart et al., 2009, p. 180). Both versions, however, have two central contentions: (1) cooperative breeding is associated with increased cognitive performance and (2) convergent evolution between humans and other cooperative breeders accounts for distinctive features of human psychology. We find little support for these ideas. Cooperative breeding does not obviously entail greater cognitive challenges than other social systems or generate selection for increased brain size. Our review of the theoretical and empirical literature on prosociality, social learning, teaching and coordination also provides no indication that these traits are restricted to or overrepresented in cooperative breeders or that their cognitive underpinning in cooperative breeders differs from those in other social animals. We have not considered other behaviours such as vocal plasticity and visual perspective-taking as the proponents of the CBH themselves acknowledge that there is no clear evidence that cooperative breeders excel in these areas (Burkart & van Schaik, 2010; for reviews of these topics see Janik & Slater, 2000; Davidson et al., 2014). A robust appraisal of the CBH will require phylogenetically controlled analyses, accounting for ecological variables such as diet and using cognitive data obtained using comparable methods; a prospect that is still a long way from being possible. However, based on the data currently available, the CBH appears to have little promise. At its core, the CBH is anthropocentric in character and taxonomic focus, reflecting its origins as an attempt to explain the distinctive cooperative tendencies and socio-cognitive abilities of humans. If we are to understand how cognition evolves, we need hypotheses rooted in the ecological reality of the challenges animals face in their natural environments.

Acknowledgements

We are grateful to Andy Russell, Shakti Lamba and Fred Ispanze for stimulating discussion and to Deborah Custance and Simon Reader for sharing their data with us. This work was supported by funding from the BBSRC (David Phillips Fellowship to A.T. BB/H021817/1) and Yale University (K.M.).

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