



Review

Cite this article: Silk JB, House BR. 2016

The evolution of altruistic social preferences in human groups. *Phil. Trans. R. Soc. B* **371**: 20150097.

<http://dx.doi.org/10.1098/rstb.2015.0097>

Accepted: 12 September 2015

One contribution of 18 to a theme issue

'The evolution of cooperation based on direct fitness benefits'.

Subject Areas:

evolution, cognition, behaviour

Keywords:

altruism, social preferences, cooperation

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The evolution of altruistic social preferences in human groups

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In this paper, we consider three hypotheses to account for the evolution of the extraordinary capacity for large-scale cooperation and altruistic social preferences within human societies. One hypothesis is that human cooperation is built on the same evolutionary foundations as cooperation in other animal societies, and that fundamental elements of the social preferences that shape our species' cooperative behaviour are also shared with other closely related primates. Another hypothesis is that selective pressures favouring cooperative breeding have shaped the capacity for cooperation and the development of social preferences, and produced a common set of behavioural dispositions and social preferences in cooperatively breeding primates and humans. The third hypothesis is that humans have evolved derived capacities for collaboration, group-level cooperation and altruistic social preferences that are linked to our capacity for culture. We draw on naturalistic data to assess differences in the form, scope and scale of cooperation between humans and other primates, experimental data to evaluate the nature of social preferences across primate species, and comparative analyses to evaluate the evolutionary origins of cooperative breeding and related forms of behaviour.

1. Explanations of human cooperation and social preferences

Cooperation among unrelated individuals, who do not share direct genetic interests in offspring, is uncommon in nature but ubiquitous in human societies. The capacity to cooperate in large groups with non-relatives has enabled humans to develop markets and trade networks, wage war, build public works and create social institutions. Human cooperation is regulated by social norms that establish standards for how people should behave in particular situations [1,2], and strengthened by punitive sanctions against those that violate social norms [3–5]. Cooperation is also supported by prosocial emotions, such as compassion and guilt, and altruistic social preferences, including a concern for the welfare of others and a preference for equity, which mediate conflicts between self-interest and altruism [6,7].

How did the capacity for large-scale cooperation and altruistic social preferences arise within human societies? One answer to this question is that human cooperation is built on the same evolutionary foundations as cooperation in other animal societies—kin selection, contingent reciprocity and mutualism—and that fundamental elements of the social preferences that shape our species' cooperative behaviour are also shared with other closely related primates [8,9]. Another possibility is that selective pressures favouring cooperative breeding have shaped the capacity for cooperation and the development of our social preferences [10–12]. Convergent evolution has produced a common set of behavioural dispositions and social preferences in cooperatively breeding primates and humans [13,14]. Finally, humans may have derived capacities for collaboration, group-level cooperation and altruistic social preferences that are linked to our interdependence and capacity for culture [15–18].

In the remainder of this paper, we evaluate these three explanations. We draw on observational data to assess the nature of cooperation in non-human primate species, experimental data to evaluate the nature of social preferences

in humans and other primates, and comparative analyses to evaluate the evolutionary origins of cooperative breeding and related forms of behaviour.

2. Form, scope and scale of altruism in non-human primates

There are important differences between humans and other primate species in the form, scope and scale of altruistic behaviour. Social grooming, alloparental care, coalitionary support and territorial defence are widely distributed across the primate order. Food sharing among adults only occurs regularly in chimpanzees (*Pan troglodytes*; [19]). The costs of most forms of altruistic behaviours are probably fairly low. For example, in chimpanzees, intergroup aggression can have lethal consequences, but chimpanzees do not launch lethal attacks unless they outnumber their victims, and there are no records of aggressors being injured [20]. The most conspicuous exception to this pattern of low-cost prosocial behaviour occurs in cooperatively breeding species, in which subordinate group members help care for the offspring of the dominant breeding pair, but do not reproduce themselves.

Cooperation in non-human primates is biased in favour of genetic relatives and reciprocating partners. In virtually all species that have been studied, when maternal kin are available they are the preferred partners for altruistic behaviours, such as grooming and coalition formation [21,22]. Biases in favour of paternal kin have been reported in a small number of species, but it is not yet clear how widespread paternal kin recognition and paternal kin biases are [21]. In a number of species, altruism is biased in favour of reciprocating partners [23]. Naturalistic observations provide evidence that animals are most likely to groom, support or share with those from whom they receive the most grooming, support and food, and that altruistic behaviour may be exchanged across currencies, and balanced over long time intervals [24]. Naturalistic field experiments also suggest that altruism is contingent on prior acts of cooperation [25]. Thus, altruism in non-human primate groups seems to be a product of kin selection and some form of contingent reciprocity.

Nearly all the altruistic behaviours that occur in primate groups involve pairs of individuals. However, intragroup coalitions and territorial defence may involve larger numbers of participants. Information about the size of intragroup coalitions is limited, but in six primate species the number of participants in coalitions ranged from two to five. In all six species, the majority of coalitions involved only two individuals (range: 58–100%; [26]). In some cases, intergroup coalitions involve all group members, but in most cases, they are limited to members of a single sex or subset of the group [27]. For example, in common marmosets (*Callithrix jacchus*) all group members participate in intergroup encounters, but the strength of their responses vary by age and sex [28]. Among chacma baboons (*Papio ursinus*) only males are involved in intergroup encounters, and the number of participants ranges from one to nine [29]. Border patrols in the large community of chimpanzees at Ngogo include on average 13 individuals (range: 3–27; [30]).

Cooperative interactions rarely extend beyond group boundaries, and social ties are usually severed after dispersal. There are a few exceptions to this rule. Male western gorillas, *Gorilla gorilla gorilla*, are generally hostile to males from other

groups, but groups headed by related silverbacks have more tolerant relationships [31]. Several primate species form multi-level societies, in which multiple separate reproductive units share a common range and coordinate their movements. Males from different reproductive units sometimes form coalitions against other males (*Rhinopithecus* [32]; *Theropithecus gelada* [33]; *Papio hamadryas* [34]). However, there is no evidence for cooperation among unfamiliar individuals from different groups that do not have a prior history of association.

There is little evidence of collective foraging in non-human primates, as individuals procure and process food independently. There is no evidence of division of labour by age or sex class. Chimpanzees are more likely to hunt when they are in groups than when they are alone [35], but at most sites there is no clear evidence of cooperation during hunts [36]. However, chimpanzees at Taï coordinate their activities in space and time, and take on complementary roles [37].

There is no systematic evidence for third party punishment in non-human primates [38,39]. Here, it is important to clarify the distinction between two kinds of punishment. Some types of punitive behaviour benefit the actor by altering future behaviour of the victim. For example, if Sylvia attacks Helen after Helen takes a bit of food from her, Helen may be less likely to steal food from Sylvia in the future. We refer to this as second-party punishment. These kinds of punitive interactions are probably common in nature [40]. However, if Beth attacks Helen after Helen steals food from Sylvia, then Beth incurs costs and Sylvia gains benefits. This type of punishment is labelled third party punishment and is a form of altruism [1].

There is growing evidence for social transmission of novel behaviours in non-human primates [41], but very little evidence of teaching [42]. Callitrichids, which provision their offspring with animal prey, seem to use food transfers to inform naive infants about the palatability of novel foods [43,44]. There is only one report of teaching in chimpanzees. In the Taï forest, where chimpanzees use heavy stones to pound open nuts on flat anvil stones, mothers respond to their offsprings' interest in nut cracking by leaving hammer stones or nuts near anvils, placing nuts in the correct position for hammering or demonstrating the correct way to hold hammer stones [45].

3. Ancestral social preferences

If human cooperation is built on the same evolutionary foundations as cooperation in other animal societies, then we would expect to find strong similarities in the social preferences of humans and our closest primate kin, chimpanzees. Observational studies are essential for documenting the form, scope and scale of altruism in nature, but they are less useful for evaluating the social preferences that shape behaviour [46,47]. Current controversy about the interpretation of food transfers illustrates this problem. Chimpanzees might share meat because they have preferences for outcomes that benefit others. Alternatively, meat sharing might occur because males benefit from maintaining ties with valuable allies or to reduce the costs of harassment. If either of the latter explanations holds, then self-interest would prompt chimpanzees to share, not a preference for outcomes that benefit others.

Behavioural economics experiments provide an important methodological tool for studying preferences that shape

behavioural decisions [48]. In these experiments ('games'), actors are presented with options that have different material pay-offs for themselves and others. The pay-off distributions in the games are structured to force trade-offs between competing preferences. For example, in the Dictator Game, the subject is given a sum of money and told that they can allocate the money to themselves and/or another individual. A subject that values only her own welfare would keep the full endowment, while one that places a positive value on the welfare of others or prefers fair allocations, would allocate some amount of the endowment to the other individual. Reputational concerns might affect the choices actors make, so participants in behavioural economics games are typically strangers who never meet and have no opportunity to communicate. Opportunities for reciprocity or retaliation might also influence choices, so most games last only one round, and partners do not change roles.

Researchers have adapted the discrete Dictator Game to examine the social preferences of chimpanzees. In this version of the game, the subject is given two options [49]. In what has come to be known as the Prosocial Test [50], one individual (the actor) is presented with a choice between two options. One option delivers a reward to the subject and an identical reward to another individual (the recipient) in an adjacent enclosure (hereafter, this is the 1/1 option). The other option delivers one reward to the subject, but nothing to its partner (the 1/0 option). Chimpanzees might prefer the 1/1 option over the 1/0 option because it produces a larger number of rewards (2 versus 1), not because it provides rewards to others. To address this possibility, a control condition is included in which there is no recipient present to receive rewards. If individuals are concerned about the welfare of others, they will prefer the 1/1 option over the 1/0 option, and their preference for the 1/1 option will be stronger when another individual is present than when they are alone. It is important to note that in the Prosocial Test, actors do not have to make a trade-off between self-interest and generosity because the actor's pay-off is the same for both options.

Chimpanzees are usually intolerant of strangers, so the Prosocial Test is limited to familiar individuals from the same social group. Also, because it would be difficult for the chimpanzees to understand the distribution of rewards to partners who are not present, the actor and recipient are present and visible to one another when decisions are made.

These modifications to the protocol potentially complicate interpretations of the results [49]. Individuals might choose the 1/1 option because they have ongoing relationships with group members outside the bounds of the experiment, even if they do not have genuine preferences for outcomes that benefit others. Prosocial choices might reflect biases in favour of kin, allies or prospective mates, or reputational enhancement. However, if chimpanzees do not choose the 1/1 option more often when another individual is present than when they are alone, we can conclude that they do not have systematic preferences for outcomes that benefit others.

The Prosocial Test has now been conducted with chimpanzees from a number of different captive populations [49,51–56], bonobos (*Pan paniscus*, [51,57]), gorillas [51] and orangutans [58] (*Pongo* spp. [58]). In all these cases, apes did not choose the prosocial option more often in the test condition than in the control condition. By contrast, children consistently differentiate between the control and test conditions when faced with the same set of choices [59,60].

It is possible that apes did not fully understand the consequences of their choices, and the results do not reflect their actual preferences. However, the subjects' understanding of the experimental procedures was confirmed in several of these studies. Thus, when presented with two options, chimpanzees and other great apes do not consistently prefer outcomes that benefit others.

There is, however, some evidence that task design may influence chimpanzees' responses in these experiments. House *et al.* [56] compared chimpanzees' performance in the standard form of the Prosocial Test with their performance in a modified version of the task which involved a single option. This procedure, which was modelled on one introduced by Burkart & van Schaik [61], was conducted with animals in their home cage. In the modified version of the task, rewards were placed in two bins outside the enclosure. When the actor pulled on a hose, the contents of the two bins became accessible, but the actor could obtain the contents of only one of the two bins. The distribution of pay-offs for the actor and recipient varied across trials (1/1, 1/3, 1/0, 0/1, 0/0). Actors pulled the hose on virtually all the trials in which their own bin was baited, but were much less likely to behave prosocially in trials in which only the recipient's bin was baited. They were about 8–10% more likely to respond prosocially when only the recipient's bin was baited than when no food was available. In an experiment conducted by Burkart *et al.* [62] with a one-choice task and 0/1 pay-off structure, chimpanzees delivered rewards to others about 13% of the time.

These experiments suggest that chimpanzees may be more likely to be prosocial when they are faced with less complicated choices. However, even when chimpanzees were faced with the single-option task, they only responded prosocially on a relatively small proportion of the 0/1 trials. By contrast, 4.5–7.1 year old Swiss children deliver rewards to others 98% of the time in 0/1 trials [62].

The only study that claims to find clear preferences for prosocial options in the Prosocial Test was conducted by Horner *et al.* [63]. In this study, chimpanzees were trained to associate different tokens with different reward distributions. If one type of token was chosen, the experimenter distributed one reward to the actor and an identical reward to another individual in an adjacent enclosure. If the other type of token was chosen, the experimenter distributed a reward only to the actor. A control condition was included in which the adjacent enclosure was empty. The chimpanzees were more likely to choose the 1/1 token than the 1/0 token when another chimpanzee was present than when they were alone.

Amici *et al.* [52] were unable to replicate the results from the token task with chimpanzees (or other great apes). Overall, the chimpanzees that they tested were no more likely to choose the 1/1 token when a partner was present in an adjacent enclosure than when they were alone. Individuals who were tested in the experimental condition (partner present) before the control condition (partner absent) showed a bias in favour of the 1/1 token, but animals tested in the control condition first did not. The order effect suggests that the animals might not have fully understood the task when they began. This possibility is supported by evidence from another series of trials which were conducted after all the experimental and control trials were completed. In these trials, subjects were able to gain access to the adjacent enclosure and collect

rewards placed there. Chimpanzees were expected to choose the 1/1 token over the 1/0 token consistently in these trials because this would double their rewards. However, a minority of subjects chose the 1/1 token more often than expected by chance. Amici *et al.* point out that Horner *et al.* always conducted the control condition after the experimental condition and did not explicitly test the chimpanzees' understanding of the task.

Taken together, these studies suggest that chimpanzees (and other great apes) do not have robust preferences for outcomes that benefit others. It is important to point out that the bar in these experiments is set very low: subjects do not need to make trade-offs between outcomes that benefit themselves and outcomes that benefit others. Subjects consistently take advantage of opportunities to maximize their own rewards, but are much less likely to take advantage of low-cost opportunities to deliver rewards to others.

Both naturalistic observations of social behaviour and experimental investigations of social preferences suggest that there are important differences between humans and other primates in the form, scope and scale of cooperation, and the psychological mechanisms that motivate individuals to help others. In the wild, primates cooperate in a relatively limited number of contexts, do not incur high costs when they provide services to others, show strong biases in favour of kin and reciprocating partners, and limit cooperative activities to pairs or small groups of familiar group members. Chimpanzees and other great apes do not consistently provide benefits to others in the Prosocial Test, suggesting that cooperation may not be motivated by generalized preferences for outcomes that favour others.

4. Convergent social preferences

According to the cooperative breeding hypothesis, mothers became dependent on the assistance of other group members to rear their offspring as hominins moved into new environments during the Pleistocene, and developed new subsistence strategies [10–12]. This hypothesis builds on evidence that human subsistence strategies differ from those of other mammals. Humans rely to a much greater extent on foods that are difficult to obtain and process, such as animal prey and underground tubers, than do other apes [63,64]. In foraging societies, women consume more calories than they produce for much of their reproductive lives, and children do not begin to acquire a substantial amount of their food themselves until their late teens. Thus, women and their offspring are subsidized by the foraging efforts of others. These subsidies enable mothers to produce costly, slow-growing offspring at relatively short intervals, and to care for more than one dependent offspring at the same time.

Hrdy argues that the growing importance of allomaternal care favoured a number of changes in human emotions and cognition, including heightened sensitivity to the needs of infants by potential caretakers. As infants became more dependent on the care that they received from alloparents, selection also favoured greater ability to elicit support from caretakers and to evaluate their intentions. Thus, cooperative breeding may have favoured the evolution of empathy and a more fully developed theory of mind.

Cooperative breeding may also have favoured the evolution of prosocial preferences and enhanced cognition in

humans [13,14]. In cooperatively breeding systems, alloparents play an active role in provisioning, protecting and caring for immatures. This may favour the evolution of 'proactive prosociality' [62], which motivates individuals to spontaneously provide benefits to others.

The link between cooperative breeding and prosocial behaviour was first supported by evidence from cooperatively breeding common marmosets, *Callithrix jacchus*. Burkart *et al.* [65] designed a version of the Prosocial Test in which subjects were presented with a choice between two pay-off distributions: 0/0 and 0/1. Pairings in the experiments were meant to replicate helping situations in the wild: older individuals were able to provide food to younger individuals, and males were able to provide food to their mates. Overall, subjects were significantly more likely to choose the 0/1 option when a recipient was present in the adjacent enclosure than when they were alone. When chimpanzees are presented with a similar set of options, they do not differentiate between test and control conditions [53,56]. Prosocial responses were not detected in two studies of another cooperatively breeding New World primate, the cotton-top tamarin (*Saguinus oedipus*; [66,67]), but did emerge in the final trials of an iterated version of the experiment in which partners were able to take turns playing the role of actor and recipient [68].

It is not clear whether differences between marmosets and tamarins or between marmosets and chimpanzees reflect meaningful species-specific differences or represent an artefact of differences in the procedures used to assess preferences. Therefore, Burkart *et al.* [62] implemented a protocol to assess prosocial behaviour in a diverse set of primates. In these 'group service' experiments, which were conducted in the home cage, food rewards were placed on a platform positioned outside the enclosure. To gain access to the rewards, one individual pulled on a handle which brought the platform to within reach. When the handle was released, the platform was retracted, and the reward became inaccessible. In the test condition, the animal that pulled on the handle could not reach the reward which was placed on the far end of the platform. Thus, animals were able to deliver rewards to others, but not to themselves. In the control condition, no rewards were placed on the platform. The frequency of pulling the platform forward in the test condition provides a group-level measure of the extent of prosociality.

The 14 non-human primate species that Burkart *et al.* tested in the group service task spanned a wide taxonomic range, and varied in the extent of alloparental care that they typically display. Their analyses show that the extent of alloparental care is closely related to the extent of prosociality, and it is a much better predictor of prosociality than other factors that have been linked to prosocial preferences: cognitive ability, degree of social tolerance, foraging coordination and social bonding. Based on these findings, Burkart *et al.* argue that 'proactive prosocial motivations therefore systematically arise whenever selection favours the evolution of cooperative breeding'.

If prosociality in both humans and callitrichids has its origins in adaptations for cooperative breeding, then it is important to consider the conditions that favoured the evolution of high levels of allomaternal care in callitrichids and consider whether the same conditions apply to humans.

The extent of allomaternal care in mammals is positively related to the degree of relatedness among group females [69]. The most extensive and costly forms of allomaternal

care are found among cooperative breeders, *sensu stricto*. These species form social groups that may include multiple adults of each sex, but only one breeding pair. All group members, including offspring from previous litters who delay dispersal, help care for the breeding pair's offspring, but do not reproduce themselves. This type of cooperative breeding has evolved independently 14 times in several groups of mammals, including callitrichid primates (marmosets, tamarins), canids and mongoose.

Phylogenetic reconstructions show that cooperatively breeding species are derived from socially monogamous ancestors [70]. The transition from social monogamy to cooperative breeding is associated with a shift from monotocy (singleton births) to polytocy (production of litters) or an increase in litter size [71]. In keeping with this, marmosets and tamarins routinely produce twins, while all other haplorrhine primates (monkeys and apes) produce single young.

Cooperatively breeding mammalian groups, including those of cooperatively breeding primates, are generally characterized by high reproductive skew and relatively long male breeding tenures which jointly create high levels of relatedness within groups [70]. Thus, most helpers are closely related to the infants that they care for. These findings strongly suggest that kin selection plays a critical role in the evolution of cooperative breeding [70].

The species that Burkart *et al.* tested in the group service task include three that are classified as cooperative breeders, *sensu stricto* [70]. Three other species are socially monogamous, and typically live in groups that contain one breeding pair and their immature offspring. The other eight species live in groups that contain multiple breeding females and have polygynous mating systems. There is a close correspondence between the mating system, alloparental care and extent of prosociality (figure 1). Thus, in non-human primates high levels of both allomaternal care and prosociality may be a product of selection favouring altruistic behaviour toward kin.

Humans are characterized by levels of allomaternal care and prosociality that parallel those of cooperatively breeding primates. For advocates of the cooperative breeding hypothesis, this implies that the adoption of cooperative breeding was also the basis for the evolution of altruistic social preferences in early hominins. However, there are several ways in which humans do not fit the profile for cooperatively breeding mammals [70,72].

- In other mammals, the shift from social monogamy to cooperative breeding is associated with polytocy, but humans typically produce single young. It might be argued that prolonged nutritional dependence after weaning is the functional equivalent of polytocy, as mothers care for several children of different ages at the same time. However, as children get older, they require progressively less care. Juveniles produce some of their own food, help care for younger children and participate in other economic activities [72,73].
- Infants are the primary beneficiaries of care and provisioning by helpers in cooperatively breeding primate groups [74,75]. In human societies, help is much more broadly distributed and food is more widely shared.
- In cooperatively breeding species there is only one breeding pair in each group, and this leads to high reproductive skew. Human groups contain multiple breeding pairs within the same social group, and much lower degrees

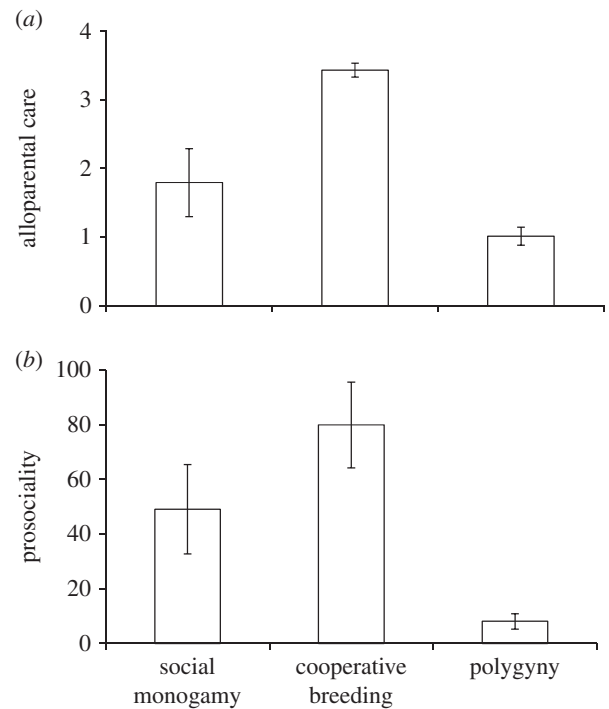


Figure 1. (a,b) Mean (and s.e.) of allomaternal care and prosociality scores for species categorized as socially monogamous, cooperatively breeding and polygynous. (Based on data from [62] provided by J. Burkart 2015, personal communication.)

of reproductive skew. A recent compilation of demographic data from 13 small scale societies shows that a minority of adults never reproduce [76].

- Levels of relatedness within cooperatively breeding groups are high. This means that nearly all group members have a genetic interest in the welfare of infants born within the group. This is not the case in human societies. Analyses of the composition of residential bands in 32 hunter-gatherer societies [77] indicate that the average size of residential groups is about 30, and each individual within the group is closely related to only a small fraction of other residents.

Thus, the form of cooperative breeding that has evolved in callitrichid primates and other cooperatively breeding mammals seems to be quite different than the form of cooperative breeding that has evolved in humans. This raises the possibility that the selective factors that have favoured the evolution of altruistic social preferences and prosocial behaviour in humans differ from the selective factors that have favoured the evolution of prosocial behaviour in other primates.

5. Derived social preferences

Derived human capacities for group-level cooperation, and the evolution of altruistic social preferences, have been linked to both the emergence of human interdependence and the coevolution of genetic and cultural adaptations [15–18]. Humans rely on culturally transmitted information to a much greater extent than other animals do, and this is clearly a key to our success as a species. Palaeontological and archaeological evidence indicates that early hominins occupied a much wider range of habitats than any of the great apes do today. They came to rely on a more diverse

set of resources, particularly animal prey, and became more reliant on a progressively more complex toolkit. This may have increased economic interdependence within groups and increased dependence on culturally transmitted information. As Hrdy [10–12] has emphasized, these changes may have made it very hard for mothers to rear their offspring on their own, and led to a number of changes in human reproductive patterns and parenting practices, including pair-bonding and extensive alloparental care.

Reliance on complex foraging techniques may have favoured economic interdependence within groups. If subsistence skills are difficult to master, it may be profitable for individuals to specialize in particular tasks, and to exchange the products of their efforts. Sexual division of labour is a universal feature of human foraging societies, as men mainly hunt and women mainly gather [78]. Sharing may also buffer the economic risks associated with hunting [79]. On some days hunters return with carcasses large enough to feed many people, but on other days they come back empty-handed. Food sharing among hunters and between hunters and foragers may have been an important form of risk pooling, and remains a fundamental feature of virtually all human societies [80]. Economic interdependence may be one of the crucial steps in human behavioural evolution, and may have favoured the evolution of cognitive skills and motivations that facilitate mutualistic collaboration [18,81].

Reliance on complex subsistence techniques may also have favoured a greater dependence on culturally transmitted information, and generated selective pressures that favour group-level cooperation [16,17]. Knowledge and subsistence technology required for foraging varied across time and space, and it would have become difficult for individuals to acquire all the information that they needed to survive on their own. Social learning may have enabled early hominins to acquire useful knowledge from skilled or prestigious group members, make incremental improvements through trial and error or insight of their own, and pass their accumulated knowledge on to others. This kind of cumulative cultural change can give rise to complex habitat-specific adaptations much more rapidly than genetic evolution can [82–84], but it has the additional consequence of causing local populations to evolve toward different equilibria. It is likely that as cultural adaptation became more and more important, the amount of variation among human groups also increased [16].

When there are multiple stable equilibria, processes that reduce the amount of cultural variation within groups will reduce the within-group component of variation and strengthen the force of selection between groups [15]. Competition between groups will favour the spread of cultural norms that enhance the welfare of the group as a whole and make it more successful in intergroup competition. Cooperative cultural norms may be strengthened by social emotions that encourage altruism to group members (e.g. empathy, inequity aversion), discourage cheating and violations of social norms (e.g. guilt, shame), and motivate punitive behaviour when norms are violated (e.g. moral outrage). Biases towards learning common or prestigious behaviours will reduce variation in conformity to cooperative social norms, as will the use of punishment to enforce norm compliance, and this further lowers within-group variation and increases the strength of selection between groups. This process could provide a path for the coevolution of cultural and genetic traits for prosociality in humans.

Models of derived human cooperative traits based on interdependence and gene-culture coevolution make two predictions about the development of prosocial preferences in children. First, the extent of variation in prosocial behaviour across groups will be more pronounced when costs of cooperation (and incentives to defect) are higher. Second, variation in the extent of prosocial behaviour will develop as children begin to acquire the social norms of their communities.

House *et al.* [60] explored these predictions in a study of the development of prosocial behaviour in 3- to 14-year old children from six societies around the world. The sample included a set of six diverse societies ranging from nomadic hunter-gatherers in the Congo Basin (Aka) to marine forager-horticulturalists from Melanesia (Yasawa Island, Fiji) and urban Americans (Los Angeles). These experiments closely parallel the Prosocial Tests conducted with chimpanzees. Children were paired with other members of their classes or communities, and one child took the role of actor and the other child took the role of the recipient. In Prosocial Test trials (1/1 versus 1/0), the actor's choices influenced the pay-offs for the recipient, but did not affect their own pay-offs. In costly sharing trials (1/1 versus 2/0), actors had to give up one reward in order to provide rewards to others. As before, a control condition was included in which there was no recipient present. In addition, we tested adults in five of the six populations using the same procedures.

Children were more likely to choose the 1/1 (prosocial) option when another child was present (test condition) than when they were alone (control condition) in both the prosocial trials and the costly sharing trials. In the prosocial game, children from all populations showed a gradual increase in prosociality with age. In the costly sharing game, children in all six populations became less likely to choose the costly prosocial option as they approached middle childhood (6–8 years of age). Population-specific variation emerged in middle childhood, and children converged toward the behaviour of adults in their own groups. The behaviour of adults in these experiments corresponded to their behaviour in a standard Dictator Game. As predicted, these findings suggest that cultural variation is magnified in tasks that require self-sacrifice, and that children become sensitive to culturally specific norms about how to behave in these situations during middle childhood.

6. Conclusion

Current evidence suggests that chimpanzees (and other great apes) cooperate in a number of contexts, but do not have robust preferences for outcomes that benefit others. Even when individuals do not need to make trade-offs between outcomes that benefit themselves and outcomes that benefit others, they do not consistently take advantage of opportunities to deliver rewards to others. However, it is important to acknowledge that this characterization may not be completely accurate. One major shortcoming of all the experimental studies of social preferences on non-human primates is that they are conducted on captive animals in laboratory settings. Efforts to devise more naturalistic experiments which could be conducted in both wild and captive settings would be very valuable.

There will probably be continuing disagreement about how to characterize the social preferences of chimpanzees and other great apes. While some emphasize continuities

between the prosocial behaviour of chimpanzees and humans in experimental settings, others emphasize the differences. However, there can be little doubt that humans cooperate more extensively, with a wider range of partners, and at greater personal cost than other apes do. At some point a sizable quantitative difference becomes a qualitative difference, and it may not be fruitful to argue about exactly where that point lies.

The form of cooperative breeding that has evolved in callitrichid primates and other cooperatively breeding mammals is substantially different than the form of cooperative breeding that has evolved in humans. Burkart *et al.* [62] may well be right that prosocial behaviour emerges whenever selection favours cooperative breeding, but this does not mean that cooperative breeding is the only factor that favours the evolution of altruistic social preferences. It seems likely that cooperatively breeding primates and humans have converged on prosociality for different evolutionary reasons and through different pathways.

The cultural group selection hypothesis helps to explain how human societies are able to combine high levels of altruism with low levels of relatedness, a combination that is not observed in other mammalian species. Cooperative breeding in human groups may be part of a broader system of group-level cooperation in which mothers receive help feeding and caring for their offspring; the families of unsuccessful hunters are fed; aid is given to the sick and the aged; and collective action problems are resolved.

If the constellation of selective pressures that have shaped prosocial behaviour in humans and cooperatively breeding mammals differ, then it is likely that human prosocial behaviour may also be motivated by a distinctive set of social preferences and psychological adaptations. As predicted by cultural evolution and interdependence models, prosociality in our species is highly influenced by social norms. Cultural variation in cooperation emerges in middle childhood, a time when children seem to become sensitive to social norms within their communities.

Further research is needed to delineate the phylogenetic and ontogenetic roots of prosocial behaviour in modern humans and to understand the psychological processes that shape our social preferences. Further work is also needed to probe the conditions that facilitate or inhibit prosocial behaviour in other primates and to chart cross-cultural variation in the development of prosocial preferences in human children.

Competing interests. The authors have no competing interests.

Funding. B.R.H. was supported by an Alexander van Humboldt post-doctoral fellowship. J.B.S.'s work was partially supported by a grant from the John Templeton Foundation to the Institute of Human Origins at Arizona State University.

Acknowledgement. We have profited from discussions of the ideas in this paper with Joe Henrich, Sarah Blaffer Hrdy, Kim Hill, Rob Boyd and Sarah Mathew.

Disclaimer. The opinions in this publication are those of the authors and do not necessarily reflect the views of the John Templeton Foundation.

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